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DEMOGRAPHIC COMPONENTS OF PHILOPATRY AND NEST-SITE FIDELITY OF PACIFIC BLACK BRANT

A

THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

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for the Degree of

DOCTOR OF PHILOSOPHY

By

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Fairbanks, Alaska

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DEMOGRAPHIC COMPONENTS OF PHILOPATRY AND

NEST-SITE FIDELITY OF PACIFIC BLACK BRANT

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Abstract: I investigated demographic components of nest-site fidelity and philopatry of Pacific black brant (*Branta bernicla nigricans*). My analyses included data I collected during summer 1990-1993, and also incorporated data obtained between 1986-1989. My studies of nest-site fidelity were limited to the Tutakoke River colony, Yukon-Kuskokwim River Delta, Alaska. Studies of philopatry and dispersal among colonies included observations at 7 breeding colonies of brant marked with tarsal tags (n = 20,147).

I observed strong evidence that philopatry of brant was female biased. Probability of breeding philopatry, which was estimated with multi-state modeling techniques, was high (> 0.9) and dispersal of adults among breeding colonies was rare. I developed an *ad hoc* estimator for natal philopatry that was unbiased by a confounding of homing, survival, and detection probabilities. Probability of natal philopatry for females was both age and density dependent. The density-dependent decline in natal philopatry may result from increased rate of permanent nonbreeding or increased probability of dispersal. Observed probability of natal philopatry for males was approximately equivalent to the relative size of their natal colony, suggesting that males pair at random with females from other colonies. Gene flow among populations of brant is largely male mediated, and I predict populations of brant will exhibit distinct mitochondrial DNAs if populations have been reproductively isolated for an adequate period of time.

Probability of fidelity to previous nest sites for adults was high (> 0.7). Probability of nest-site fidelity was affected by previous nesting success, age, and availability of nest sites. Phenology of nesting, nest-site selection, and clutch size of brant was affected by

spring snowmelt. Dispersal of brant from traditional nest sites in years with late springs may represent a tradeoff between site fidelity and timing of nest initiation. Movement of young females from natal nest sites was a mechanism for colony expansion. I observed little evidence that site fidelity was advantageous, and concluded that quality of individual bird, environmental conditions, and demographic status may be more important determinants of breeding performance.

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PREFACE

This thesis is written in 4 separate chapters that are formatted for the intended journal. The first chapter was published in the *Journal of Applied Statistics*. Chapters 2 and 3 were submitted to *Condor*, and Chapter 4 is intended for publication in *Ecology*. Although this thesis is single authored, coauthors are included for each individual manuscript. The "we" in each chapter therefore refers to the authors listed for each paper.

Although this thesis reflects a considerable amount of individual thought and effort, this work would not have been possible and would have been a lot less enjoyable without the cooperation and helpful assistance of numerous individuals. My major advisor, James Sedinger, not only provided helpful assistance and guidance throughout all phases of my thesis, but he and his family offered their unconditional friendship. The Sedinger's home cooking during the holidays was particularly enjoyable. Committee members Dirk Derksen, Eric Rexstad, Kent Schwaegerle, and Gerry Shields provided valuable guidance and were positive role models for my professional development. Gerry Shields was particularly patient and supportive of my genetic studies in his laboratory. Eric Rexstad greatly influenced my professional goals and was always available when I needed a "sounding-board." Numerous members of the faculty and staff of the Department of Biology and Wildlife and Institute of Arctic Biology were supportive of my studies.

Fellow graduate students, Mike Eichholz, Paul Flint, Maggie MacCluskie, and Joel Schmutz provided lively discussions, constructive criticism, and their friendship. Competent and enthusiastic assistance during 4 years of field work on the Yukon Delta

N.W.R. was provided by; John Barbrick, John Chakuchin, Nate Chelgren, Wayne Don, Mike Eichholz, Peter Freshman, Sergei Kharitonov, Irina Kharitonov, Philip Kugzruk, Tim Obritschkewitsch, Christa Mulder, Thomas Olson, Brian Person, Delia Person, Robert Rockwell, Tawney Rodgers, Roger Ruess, and Steve Sindelir. The logistical support provided by the staff of the Yukon Delta N.W.R. was essential for completion of the field work. Air taxi service and food resupplies provided by George Walters were particularly essential. Terry Armstrong and Jim Hines (Canadian Wildlife Service) provided valuable logistical support for my work on brant at the Anderson River, N.W.T., Canada. Bob Ritchie (Alaska Biological Research), Betty Anderson (ABR), John Rose (ABR), Philip Martin (Ecological Services, U.S. Fish and Wildlife Service), and Steve Johnson (LGL Ltd.) provided logistical support for my work on the North Slope of Alaska and shared their data. Jim Helmricks and his family were gracious hosts and guides during my studies at the Colville River Delta. Dave Ward and Karen Bollinger of the Alaska Science Center, NBS provided valuable data on brant from Colville River, Teshekpuk Lake, and Wrangell Island.

Finally, I would like to thank my parents, Ed and Rosemary Lindberg for emotional and sometimes financial support during my graduate and college career that now spans 15 years. My partner of 8 years, and now wife of almost 2 years, Maggie MacCluskie, has lived through both the highs and lows of my graduate studies and was supportive and caring during even the worst of times. Without her, this endeavor would have been much more challenging and less rewarding.

Cooperation and collaboration are important components for analyzing and interpreting data on brant spanning 10 years and geographic areas ranging from Anderson River, N.W.T., Canada to Baja California, Mexico. Every chapter of this thesis therefore has multiple-authors. I alone, however, take full responsibility for any errors.

INTRODUCTION

Movement of individuals between breeding sites and among breeding colonies has important implications for the dynamics and genetic structure of populations (see review by Rockwell and Barrowclough 1987). Although numerous theoretical models have been developed to examine demographic and genetic consequences of animal movements (e.g., Endler 1977, Rockwell and Barrowclough 1987, Pulliam 1988), empirical studies of animal movements are more limited because of logistical constraints associated with this type of research (Barrowclough 1980, Slatkin 1987, Rockwell and Barrowclough 1987). For a vagile group of organisms such as birds, quantitative studies of immigration and emigration are particularly challenging. As a result, most studies of philopatry in birds have been limited to single study sites and estimates of philopatry are plagued by a confounding of homing, survival, and detection probability (Greenwood and Harvey 1982, Anderson et al. 1992, Johnson et al. 1992). Furthermore, potential benefits of site fidelity rarely have been measured, as individuals dispersing from breeding sites are rarely found, or assumed to be dead.

Black brant present a unique opportunity to study dynamics of site fidelity and philopatry in an avian population. These birds nest in discrete colonies in coastal areas of western and northern Alaska, western Arctic Canada, and eastern Russia (Bellrose 1980). Brant breeding at these colonies are easily approached and repeated observations of dispersing and philopatric individuals can be obtained. Recent studies of brant were initiated in 1984, motivated by concerns of declining number of brant observed over the

last 2 decades (Sedinger et al. 1994). Between 1985 and 1993, > 32,000 brant were banded with individually coded tags at 5 major breeding colonies and 3 areas used by molting brant. These marked brant have been reencountered (observed or recaptured) at 7 major breeding colonies, several smaller (<100 pairs) colonies located on the Yukon-Kuskokwim Delta, Alaska, all molting areas, as well as lagoons used by brant during migration between summer breeding areas and wintering sites in Baha of California, Mexico. This intensive research effort has resulted in an increased understanding of life-history, demographic, and genetic components of the biology of these birds. My research emphasizes dynamics of site fidelity and philopatry of brant.

My goals were to estimate probability of fidelity of brant to nest sites within a colony and philopatry of brant to specific breeding colonies. Furthermore, I examined potential factors affecting probability of fidelity or philopatry and potential consequences of dispersal. Specifically, I estimated probabilities of natal and breeding philopatry for brant from the Tutakoke River colony. Observations of brant at other breeding colonies were used to assess sex-biased differences in patterns of philopatry and to examine gene flow among breeding colonies. I examined the effects of age and density on probability of natal philopatry. I estimated fidelity of brant to nest sites by observing marked brant at the Tutakoke River. I examined the effects of age, nest success, environmental factors, and reproductive success on future probability of fidelity. I investigated potential benefits of site fidelity by comparing nest success and reproductive performance of brant exhibiting fidelity and those dispersing to new nest sites.

Estimating Nest Site Fidelity of Adult Female Black Brant With Multistate Modeling and Geographic Information Systems[1]

SUMMARY Nest site fidelity of adult female black brant breeding at the Tutakoke River, Alaska was evaluated from 1987-1993 by recording nest locations of brant marked (approx. 1,500) with individually coded tarsal tags. We used 2 approaches to study fidelity. First, we examined fidelity to 4 geographic strata within the Tutakoke River colony. For our second analysis approach, we used ARC/INFO to map and measure distances between successive nesting attempts and then estimated the probability of fidelity to within 200m of the previous nest site. We used program MSSURVIV to estimate movement probabilities and to test hypotheses about fidelity. Both of our analysis approaches indicate that female black brant exhibit a high (>0.72) probability of fidelity to previous nest sites. Our estimates of fidelity were not biased by the confounding of detection, survival, and movement probabilities that have plagued previous studies of fidelity.

[1]Published as Lindberg, M. S., J. S. Sedinger, and E. A. Rexstad. 1995. Estimating nest site fidelity of adult female black brant with multi-state modeling and geographic information systems. Journal of Applied Statistics 22:725-735.

1 Introduction

Waterfowl (Anderson et al. 1992) and some sandpipers (Oring and Lank 1984) are unusual among birds in that females, rather than males, tend to exhibit fidelity to breeding areas (Greenwood 1980). Numerous waterfowl studies (see review by Anderson et al. 1992) have documented female biased philopatry to breeding areas. However, few studies have examined fidelity of females to specific breeding sites and most of these studies have been limited to cavity nesting species (Dow and Fredga 1983, Gauthier 1990, Hepp et al. 1989). More importantly, estimates of fidelity are generally plagued by a confounding of dispersal, mortality, and detection probability, which results in an underestimate of fidelity. Return rate, the product of survival, homing, and detection probability, is the most frequently estimated parameter in studies of fidelity (Anderson et al. 1992). In studies where homing rate is estimated, survival rates are generally estimated using ad hoc approaches.

Fidelity and dispersal are important components of the ecology of waterfowl populations. Emigration and immigration, like death and recruitment, not only affect the size of populations, but also influence the genetic structure of populations. Through site familiarity, females that exhibit fidelity may experience increased feeding efficiency and nest success, and proximity to kin may reduce aggressive interactions (Anderson et al. 1992). Therefore, accurate estimates of fidelity are essential to understand the ecology and evolutionary biology of waterfowl populations, and to make informed management decisions. Anderson et al. (1992) suggested that more accurate estimates of female

fidelity might be obtained through the use of mark-recapture statistical approaches; we investigated this potential through the study of a marked population of black brant (*Branta bernicla nigricans*).

Between 1987-1993 we studied nest site fidelity of black brant nesting at Tutakoke River, Alaska. Black brant are a small (approx. 1.5kg) goose that breeds in discrete colonies of 50 to 10,000 pairs along the coast of Alaska, Western Canada, and Russia (Fig. 1). These geese offer several advantages for studying fidelity of birds to specific breeding sites. First, since 1986, >12,500 brant have been marked at Tutakoke River with individually coded tarsal tags that are legible at 300m with spotting scopes. Second, dispersal of adult females among colonies is rare (Lindberg unpubl. data); therefore, estimates of survival rates are not biased by emigration. Finally, nesting brant are easily approached and observed, and since 1987 intensive observations of marked brant have provided a history of nest locations for individual females.

We used a multistate modeling approach, which was originally proposed by Arnason (1972, 1973) and Seber (1982, p. 555), to obtain parameter estimates and to test specific hypotheses about fidelity of female black brant to nest sites. This technique was used by Hestbeck et al. (1991) to study winter site fidelity of Canada geese (*Branta canadensis*), Nichols et al. (1992) to estimate transition probabilities for weight classes of meadow voles (*Microtus pennsylvanicus*), and studies of transitions among breeding classes have been proposed (Brownie et al. 1993). Using program MSSURVIV we obtained estimates of fidelity and dispersal probabilities unbiased by a confounding of

mortality, dispersal, and detection probability.

2 Methods

During May and June 1987-1993, we mapped the nest locations of individually marked female black brant nesting at the Tutakoke River, Alaska (Fig. 1) on aerial photos of the study area. We transcribed all nest locations to 1:6,500 scale enlargements of NASA U-2 color infrared photos of the study area. From the enlarged color infrared photos, we digitized nest locations with ARC/INFO on an UNIX workstation. For digitizing, we used control points from a coverage of the Tutakoke River area that was previously scanned from NASA U-2 photos (Tande and Jennings 1986). We assessed accuracy of our digitized nest locations by comparing distances between nest locations we measured in the field (1989-1993) and distances obtained from digitized points for the same nest locations. We compared known distances (i.e., measured distances) and distances obtained after digitizing using simple linear regression.

From a sample of females for which we obtained nest locations in consecutive years (1987-1993), we calculated mean and maximum distance moved between consecutive nesting attempts. To avoid pseudoreplication, we used only the first between-year distance for females that were observed in more than 2 consecutive years.

We used 2 approaches to study nest site fidelity of female black brant at Tutakoke. First, we divided the Tutakoke colony into 4 geographic strata (A-D) based on natural boundaries (i.e., rivers and tidal sloughs) (Fig. 2). Although these boundaries were based on geographic features, these strata also represent variations in nest densities and habitat

types. For example, stratum A (Fig. 2) was a portion of the colony that dramatically increased in number of nesting pairs (from approx. 1 nest/ha to 13 nests/ha) between 1987 and 1993. This portion of the colony was characterized by islands of vegetation surrounded by tidally inundated mud flats. In contrast, stratum D was a lower density (approx. 5 nests/ha) nesting area characterized by large inland lakes and extensive grass and sedge meadows. Strata B and C were characterized by moderate (approx. 7 nests/ha) and high (approx. 10 nests/ha) nesting densities, respectively, and both strata had numerous lakes with interspersed meadows. For each year a female was observed nesting at Tutakoke, we recorded the stratum of her nest site. Therefore, a female observed nesting in stratum C in 1987, stratum C in 1989, stratum B in 1993, and not seen in 1988, 1990, 1991, or 1992, had a capture history of C0C000B.

For the second analysis we recorded the distance females moved between consecutive nest locations and defined the state of a female at time i relative to her nest location at time i-1. Therefore, we scored the state of a female at time i as 1 if she moved <200m from her nest site at time i-1 or 2 if she moved $\geq$ 200m from her nest site at time i-1. Because the state of a female was unknown at initial capture, we conditioned our analysis on the second capture of females (i.e., capture histories for females started with the second consecutive capture). In addition, if the state of a female could not be determined on capture at time i, because the nest location at time i-1 was unknown, we considered the female undetected at time i. Therefore, detection probabilities reflect the joint probability of being observed and having a definable state. Only 5 females initially

observed in 1987 were also observed in 1988, therefore, we restricted our analysis to 1989-1993. Although a 200m radius of fidelity seems arbitrary, we believe females that moved this distance were exposed to a new environment (e.g. new neighbors and potentially different habitat conditions) and therefore had abandoned fidelity to a particular nest site. We determined distance between nest locations using Universal Transverse Mercator grid coordinates from digitized nest locations.

We used a multistate modeling approach described by Brownie et al. (1993), which is available in program MSSURVIV, to analyze both data sets described above. This analysis approach is similar to Jolly-Seber analysis (Pollock et al. 1990); however, capture histories for marked individuals include not only the time of capture, but also the stratum of capture (Brownie et al. 1993). Parameter estimates and hypothesis tests were obtained using program MSSURVIV on a UNIX workstation. For each analysis we obtained maximum likelihood estimates of the following parameters; p_i^s, the probability of capture at time i for a bird in stratum s at time i; s_i^r, the probability of being alive and returning to the Tutakoke colony at time i+1 for a bird alive and in stratum r at time i; and Ψ_i^{rs}, the probability of being in stratum s at time i+1 for animals that were in r at i and survived to i+1. For our analysis we considered only Arnason-Schwarz models ("memory-less" models), that is, models based on Markovian transitions where the stratum occupied at time i+1 is only dependent on the stratum occupied at i, not the stratum occupied at any previous time (Brownie et al. 1993).

Our approach to analysis was to first attempt to reduce the number of parameters

in our models by constraining capture probabilities (p_i^s) and survival probabilities (s_i^r) equal over years (p^t, s^t), strata (p_i, s_i), or both years and strata (p, s), while movement probabilities remained both year and stratum specific (Ψ_i^m). This step-down approach reduces the variance of the estimated parameter of interest (i.e., $\hat{\Psi}_i^m$), thereby increasing test power (Lebreton et al. 1992). Combinations of year and stratum constraints on capture and survival parameters resulted in 16 models that we considered for both the geographic- and distance-based analysis.

We selected the most parsimonious model, with respect to capture and survival probability constraints, based on Akaike information criteria (AIC, Akaike 1973). When models differed by <10 units, we also considered likelihood ratio tests (LRT) between nested models. The model selected was further constrained to test specific hypotheses about movement probabilities and to obtain estimates for all 3 parameter groups. Again, we used AIC and LRTs between nested models for hypothesis testing, and χ^2 goodness-of-fit tests to evaluate model fit.

3 Results

The difference between measured nest distances and those distances obtained from digitized points averaged -2.09m ($\widehat{SE}$ = 0.33, n = 736; r^2 = 0.48). Between consecutive years females moved on average 401.0m ($\widehat{SE}$ = 36.0 , n = 371) and distances moved between pairs of consecutive years were not different ($F_{5,365}$ = 1.33, P = 0.252). The distribution of dispersal distances was highly leptokurtic (Fig. 3), >50% of the brant moved <200m and the maximum detected distance moved between consecutive nest

attempts was 4655m.

3.1 Fidelity to geographic strata

From 1987 to 1993 we recorded the nesting strata of 1,452 individual females, totalling 2,532 observations. Of the 16 reduced parameter models considered, model $p_i^s S^r \Psi_i^m$, had the lowest AIC value (Table 1). This model allowed capture probability to vary over years and strata and constrained survival probability equal over years. In addition, the likelihood ratio test between model $p_i^s S^r \Psi_i^m$ and the model with the next lowest AIC value ($p_i S^r \Psi_i^m$) (Table 1) rejected ($\chi^2_{18} = 49.345$, $P = 0.0001$) the reduced model. We therefore maintained model $p_i^s S^r \Psi_i^m$ conditions for p and s for hypothesis tests and constraints on Ψ.

We tested the hypothesis that movement among strata was equally probable by comparing model $p_i^s S^r \Psi_i^m$ to a model ($p_i^s S^r \Psi_i^r$), which constrained the 3 movement probabilities (1 of the 4 movement probability is estimated by subtraction) equal within a stratum (e.g., $\Psi_i^{AB} - \Psi_i^{AC} - \Psi_i^{AD} - 0.25$; ... ; $\Psi_i^{DB} - \Psi_i^{DC} - \Psi_i^{DD} - 0.25$) (Fig. 4). Because model $p_i^s S^r \Psi_i^r$ was rejected ($\chi^2_{69} = 1392.0$, $P < 0.001$, Fig. 4), we concluded that movement probability was not equally probable. Therefore, we considered 5 additional models that decomposed movement probability into fidelity probability (Ψ_i^m) and dispersal probability (Ψ_i^m) and generally constrained these parameters equal over years (Ψ^r, Ψ^m), strata (Ψ_i^r, Ψ_i^s), or both years and strata (Ψ^r, Ψ^s). All reduced models fit the data ($P > 0.05$) except the model ($p_i^s S^r \Psi^r \Psi^s$) that constrained fidelity and dispersal probability equal

over both time and strata (Fig. 4). Because model $p_i^s S^r \Psi^m$ had the lowest AIC value we concluded that fidelity and dispersal probabilities were stratum specific, but equal over years. However, a discrepancy between the AIC values and LRT may indicate a year specificity of movement probabilities. Even though model $p_i^s S^r \Psi^m$ had an AIC value 36 units lower than model $p_i^s S^r \Psi_i^m$, the LRT between these models rejected ($\chi^2_{62} = 78.07$, $P = 0.033$) the reduced model. We chose to present parameter estimates from model $p_i^s S^r \Psi^m$ because this model had the lowest AIC value and 57 fewer parameters than $p_i^s S^r \Psi_i^m$. Additionally, parameter estimates for model $p_i^s S^r \Psi_i^m$ parameters were estimated to only 1 significant digit and were therefore difficult to interpret.

Capture probability estimates from model $p_i^s S^r \Psi^m$ were lowest for stratum D ($\hat{p}^D = 0.221$, $\widehat{SE} = 0.001$, $n = 6$) and averaged 0.452 ($\widehat{SE} = 0.001$, $n = 18$) for the remaining 3 strata. Survival probability was also lowest for stratum D (0.580, $\widehat{SE} = 0.066$), but was similar for strata A, B, and C ($0.763 \leq \hat{S}^r \leq 0.787$, all $\widehat{SE}$'s < 0.032, Table 2). Probability of fidelity to a stratum was >0.74 for all 4 strata and exceeded 0.94 for stratum A (Table 2).

3.2 Fidelity to a 200m radius of previous nest site

From 1989-1993 we mapped the nest locations of 247 individual females, totaling 385 observations. As in the geographic based analysis, we considered 16 models that constrained capture and survival probabilities. These models had the same structure as described above, constraining capture and survival probabilities equal over strata, years, or

both strata and years. Based on AIC we selected model $p_i S \Psi_i^{\pi}$ (Table 3), which constrained capture probabilities equal over strata and survival probabilities equal over strata and years. Although other researchers (Barrowclough 1978) have reported a decline in detection probability with increasing dispersal distance, we were unable to detect differential resighting probability as a function of dispersal distance (i.e., $\hat{p}$ constant over strata). We maintained model $p_i S \Psi_i^{\pi}$ constraints on p and S for further constraints on Ψ.

In addition to model $p_i S \Psi_i^{\pi}$, we considered 3 other models that constrained movement probability equal over years, strata, or both years and strata (Fig. 5). Based on AIC values and LRTs we selected model $p_i S \Psi^{\pi}$, which constrained movement probabilities equal over years, but allowed these probabilities to vary over strata (Fig. 5). Under this model capture probabilities, which reflect the joint probability of being observed and having a definable state, ranged from 0.598 ($\widehat{SE}$ = 0.244) in 1990 to 0.853 ($\widehat{SE}$ = 0.071) in 1992, and survival probability equaled 0.591 ($\widehat{SE}$ = 0.049). Fidelity probability between i and i+1 was higher ($\chi_1^2 = 8.262$, $P = 0.004$; LRT model $p_i S \Psi^{\pi}$ vs model $p_i S \Psi$) for female brant that moved <200m between i-1 and i ($\hat{\Psi}^{11} = 0.728$, $\widehat{SE}$ = 0.049) than for females that moved ≥ 200m between i-1 and i ($\hat{\Psi}^{21} = 0.476$, $\widehat{SE}$ = 0.069) (Table 4). The high ($\hat{\Psi}^{22} = 0.524$, $\widehat{SE}$ = 0.069) proportion of females that moved ≥ 200m between nest sites in 2 consecutive nesting attempts suggests that females returned to their previous nest site or that a portion of the population is composed of

females that moved repeatedly.

4 Discussion

Under our definitions of fidelity, female black brant returned to specific nest sites with high ($\hat{\Psi}^{\pi}$>0.72) probability. We believe the multistate modeling approach we applied not only provided accurate parameter estimates, but also increased our understanding of the patterns of fidelity exhibited by female black brant nesting at Tutakoke River. Although we did not examine the possible consequences and causes of site fidelity to breeding brant, the high rates of fidelity that we observed suggest that benefits could exist. Dow and Fredga (1983) and Gauthier (1990) observed some breeding benefits to females that exhibit fidelity to nest boxes. Anderson et al. (1992) suggested that site fidelity could increase feeding efficiency and decrease aggressive encounters with new neighbors. Dow and Fredga (1983) also suggested that nest success in year i may influence fidelity probability in year i+1. The indication of year specificity in movement probability for our geographic based analysis suggests that certain factors may influence patterns of fidelity. Although we observed only small variations in nest success since 1987, patterns and timing of snow melt were quite variable during our study and we believe this may influence nest site selection.

Wright (1943) and Endler (1977) have proposed theoretical models for speciation and clinal variation in populations that exhibit continuous breeding distributions. However, there is little empirical evidence to evaluate their models. The high rates of fidelity we observed, particularly for the distance based analysis, basically describe

"neighborhoods" as defined by Wright (1943). These neighborhoods may not be a mechanism for speciation, but high probability of fidelity could lead to heterogeneity in the genetic structure of a breeding population. Further research into natal site fidelity of black brant will increase our understanding of the relatedness of individuals nesting in a particular portion of the colony.

We presented 2 approaches to analyzing fidelity of a bird that exhibits a continuous nesting distribution. Although fidelity was defined in different ways for these approaches, both analyses provided evidence that female brant are faithful to nesting areas. However, researchers should realize that our second analysis approach, which defined the state of individual relative to i-1, required that birds be captured on at least 2 consecutive occasions and is therefore data intense. The choice of an analysis approach may depend more on the question of interest, particularly with regard to factors influencing fidelity. We view these 2 approaches as a means of addressing both the "site" (i.e., geographic) component of fidelity and the "state" (i.e., behavioral) component of fidelity. For example, the geographic based analysis approach seems more appropriate for investigating the effects of broad scale environmental factors (e.g., snow melt, habitat types) on fidelity, whereas the distance based analysis could be used to investigate the effect of demographic factors (i.e., nesting success or age) on fidelity. In addition, the potential for an interaction of these factors can not be ignored and data must therefore be coded accordingly. However, researchers must consider the dramatic proliferation of parameters as model complexity increases and innovative methods must be used to reduce parameter

space and variance of parameter estimates.

Finally, our definitions of fidelity required that we categorize nesting strata for a bird that exhibited a continuous nesting distribution. Our defintions of strata were based on our knowledge of environmental (e.g., snowmelt patterns, habitat characteristics) and behavioral (e.g., territory size, predator mobbing) factors that likely influence nest distribution patterns in black brant and our ability to accurately map nest locations. Although the distribution of dispersal distances provides valuable descriptive information (see Fig. 3), we believe that the concept of fidelity still requires a definition of how close an individual must return to be considered philopatric. Different strata boundaries may provide insights about threshold distances for fidelity, but specific hypothesis tests about fidelity (e.g., comparisons of fidelity probabilities for different age or sex classes) should not be affected by different boundary definitions.

In future analyses we will explore the fidelity probability of other age and sex classes of brant. Specifically we are interested in the fidelity of female and male brant to natal nest sites and a comparison of fidelity probability of adult males and females. Finally, we will explore the potential causes and consequences of nest site fidelity by considering the effects of snow melt patterns and nesting success. This analysis will be accomplished by treating these factors as covariates in an ultrastructure design or by expanding our state definitions (e.g., successful breeders that disperse).

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Table 1. Models with capture and survival probability constraints and relevant statistics for analysis of fidelity of female black brant to 4 geographic strata, Tutakoke River, Alaska.

Model	AIC[a]	NPAR[b]	GOF[c]
$pS\Psi_i^m$	931	71	0.013
$p_iS\Psi_i^m$	851	76	0.223
$p^sS\Psi_i^m$	872	74	0.634
$p_i^sS\Psi_i^m$	847	94	0.995
$pS_i\Psi_i^m$	857	76	0.162
$pS^r\Psi_i^m$	884	74	0.423
$pS_i^r\Psi_i^m$	879	93	0.818
$p_iS_i\Psi_i^m$	861	77	0.127
$p_iS^r\Psi_i^m$	815	79	0.834
$p_iS_i^r\Psi_i^m$	894	94	0.823
$p^sS_i\Psi_i^m$	846	79	0.963
$p^sS^r\Psi_i^m$	861	77	0.840
$p^sS_i^r\Psi_i^m$	862	96	0.970
$p_i^sS_i\Psi_i^m$	836	95	0.928
$p_i^sS^r\Psi_i^m$	802	97	0.995
$p_i^sS_i^r\Psi_i^m$	826	112	0.998

[a] Akaike information criteria.
[b] No. of parameters in the model.
[c] *P*-values for χ^2 goodness-of-fit tests, without pooling.

Table 2. Survival, fidelity, and dispersal probability estimates for model $p_i^s S^r \Psi^{\pi}$, fidelity of female black brant to 4 strata, Tutakoke River, Alaska.

Stratum	$\hat{S}^{r}$ [a]	SE	$\hat{\Psi}^{\pi}$ [b]	SE	$\hat{\Psi}^{\pi}$ [c]	SE
A	0.763	0.021	0.947	0.010	0.053	0.010
B	0.787	0.032	0.835	0.027	0.165	0.027
C	0.780	0.029	0.750	0.037	0.250	0.037
D	0.580	0.066	0.750	0.061	0.250	0.061

[a] $\hat{S}^{r}$, estimated survival probability. $\hat{S}^{r}$ was stratum specific, but constant over years.
[b] $\hat{\Psi}^{\pi}$, estimated probability of fidelity to the same stratum between consecutive years. $\hat{\Psi}^{\pi}$ was stratum specific, but constant over years.
[c] $\hat{\Psi}^{\pi}$, estimated sum of the probabilities of dispersal from the stratum occupied in year i. $\hat{\Psi}^{\pi}$ was specific to the stratum (r) occupied in year i, but constant over years.

Table 3. Models with capture and survival probability constraints and relevant statistics for analysis of fidelity of female black brant to within 200m of previous nest site, Tutakoke River, Alaska.

Model	AIC[a]	NPAR[b]	GOF[c]
$pS\Psi_i^n$	123.1	10	0.024
$p_iS\Psi_i^n$	122.2	13	0.049
$p^sS\Psi_i^n$	123.4	11	0.027
$p_i^sS\Psi_i^n$	127.3	17	0.030
$pS_i\Psi_i^n$	124.9	13	0.026
$pS^r\Psi_i^n$	123.8	11	0.024
$pS_i^r\Psi_i^n$	131.3	17	0.011
$p_iS_i\Psi_i^n$	124.3	15	0.043
$p_iS^r\Psi_i^n$	123.2	14	0.046
$p_iS_i^r\Psi_i^n$	130.9	19	0.017
$p^sS_i\Psi_i^n$	126.1	14	0.024
$p^sS^r\Psi_i^n$	122.3	12	0.040
$p^sS_i^r\Psi_i^n$	130.8	18	0.015
$p_i^sS_i\Psi_i^n$	126.9	18	0.039
$p_i^sS^r\Psi_i^n$	129.3	18	0.022
$p_i^sS_i^r\Psi_i^n$	132.8	22	0.017

[a] Akaike information criteria.
[b] No. of parameters in the model.
[c] *P*-values for χ^2 goodness-of-fit tests, without pooling.

Table 4. Fidelity and dispersal probability estimates for model $p_i S^{r}\Psi^{\pi}$, fidelity of female black brant to within a 200m radius of previous nest site, Tutakoke River, Alaska.

Stratum	$\hat{\Psi}^{\pi a}$	$\widehat{SE}$	$\hat{\Psi}^{\pi b}$	$\widehat{SE}$
1	0.728	0.049	0.272	0.049
2	0.476	0.069	0.524	0.069

[a] $\hat{\Psi}^{\pi}$, probability of fidelity at i+1 for a female that moved <200m between her nest site at i-1 and i (stratum 1) or moved ≥ 200m between her nest site at i-1 and i (stratum 2).
[b] $\hat{\Psi}^{\pi}$, probability of dispersal at i+1 for a female that moved <200m between her nest site at i-1 and i (stratum 1) or moved ≥ 200m between her nest site at i-1 and i (stratum 2).

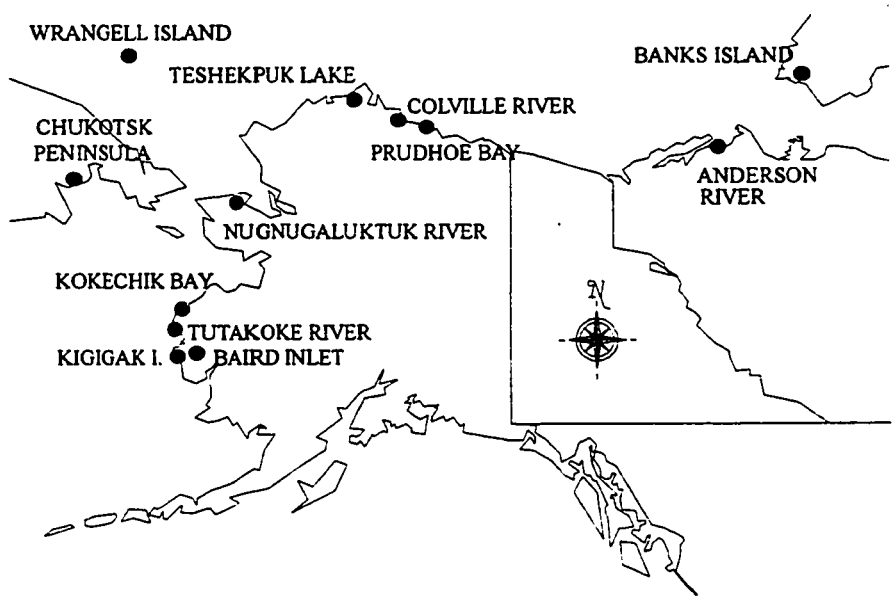

Fig. 1. Location of black brant breeding and molting areas.

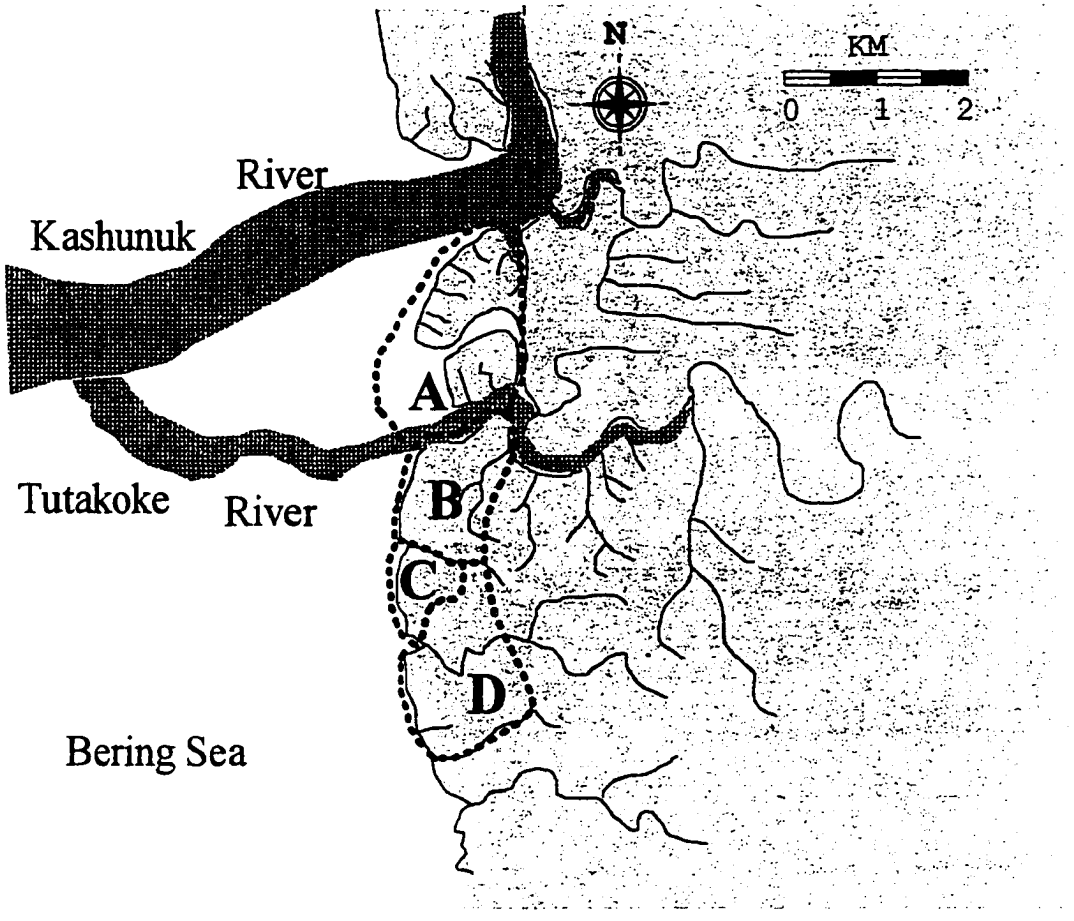

Fig. 2. Location and approximate boundaries of 4 strata (A-D) within the Tutakoke River black brant colony.

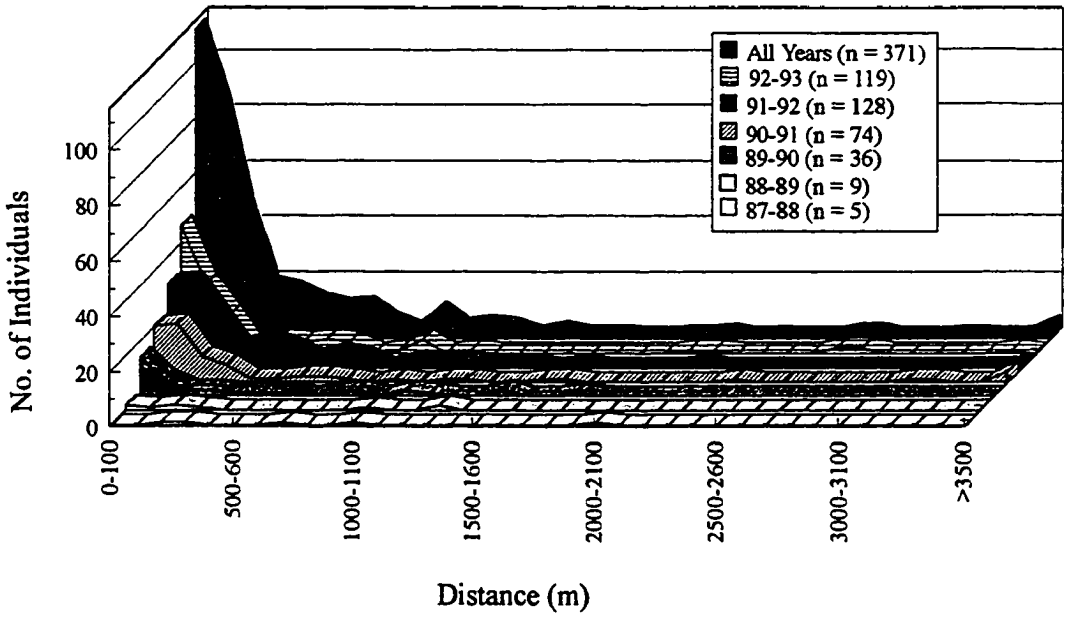

Fig. 3. Distance moved between nest sites in consecutive years by female black brant, Tutakoke River, Alaska, 1987-1993.

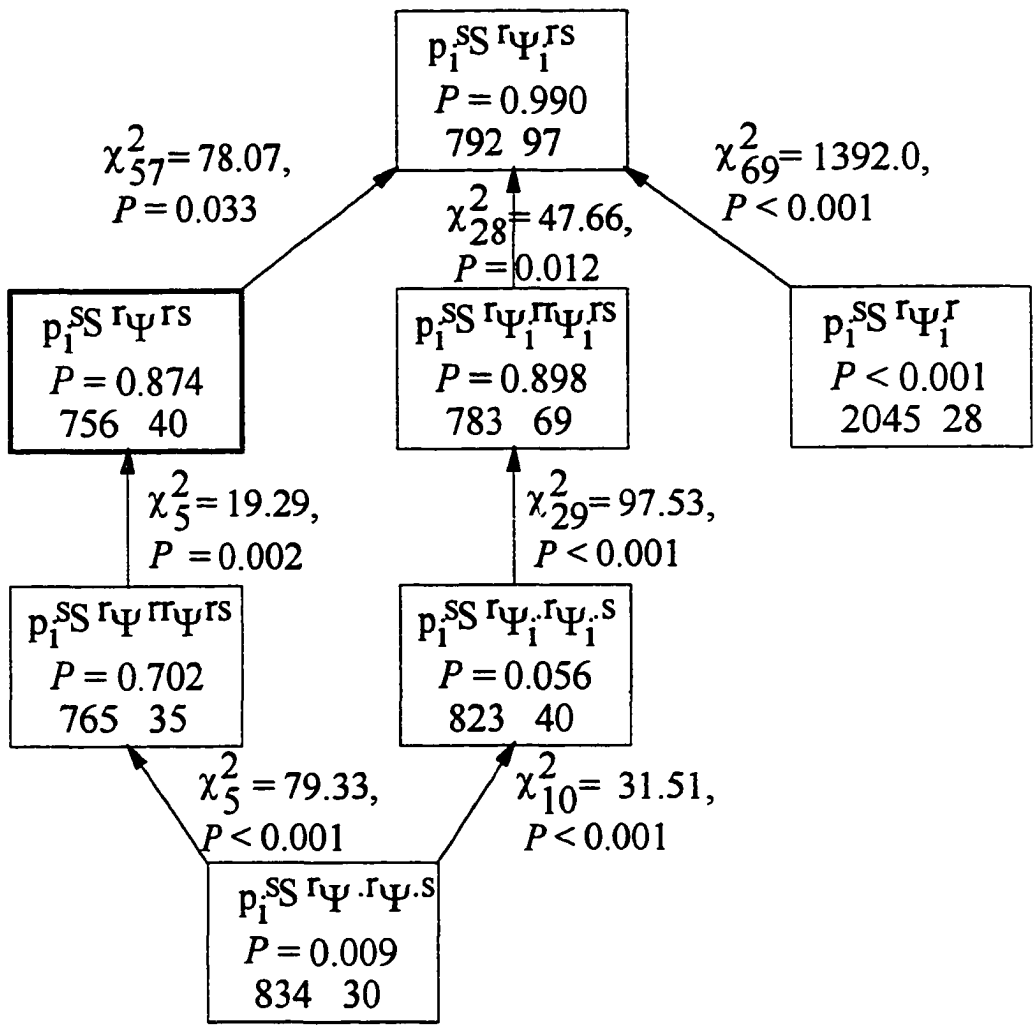

Fig. 4. Model constraints and hypothesis tests for stratum-based fidelity analysis. Model names and constraints are shown at the top of the box, chisquare goodness-of-fit tests are shown in the center of the box, Akaike information criteria values are shown in the lower left corner, and number of parameters is shown in the lower right corner. Lines between models illustrate nesting and arrows illustrate results of likelihood ratio tests. Chisquare values for likelihood ratio tests are presented near lines. Bolded box is model selected based on Akaike information criteria.

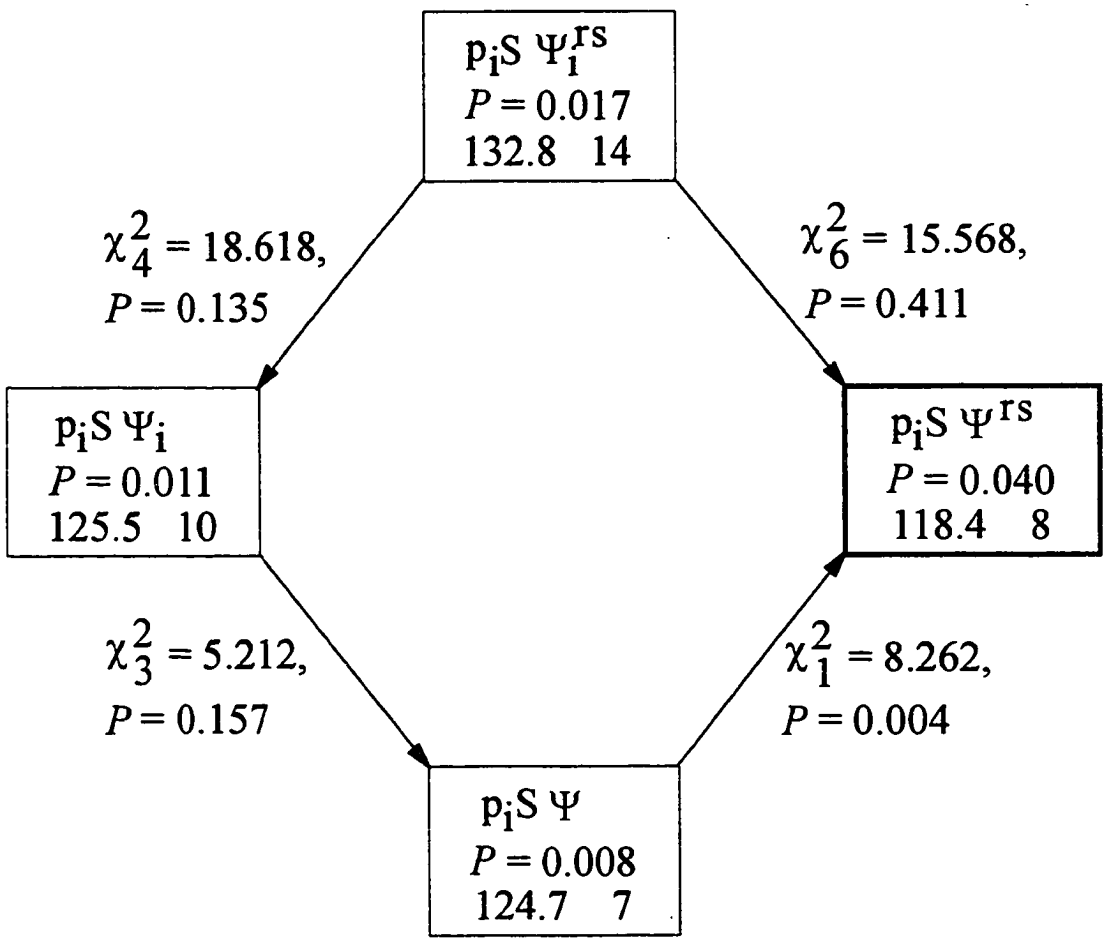

Fig. 5. Model constraints and hypothesis tests for distance-based fidelity analysis. Model names and constraints are shown at the top of the box, chisquare goodness-of-fit tests are shown in the center of the box, Akaike information criteria values are shown in the lower left corner, and number of parameters is shown in the lower right corner. Lines between models illustrate nesting and arrows illustrate results of likelihood ratio tests. Chisquare values for likelihood ratio tests are presented near lines. Bolded box is model selected based on both Akaike information criteria and likelihood ratio test.

DYNAMICS OF NEST-SITE FIDELITY IN BLACK BRANT[1]

Abstract. Empirical tests of ecological advantages of site fidelity in birds are few because consequences of dispersal are rarely measured. We examined the relationship between dispersal distance between consecutive nesting attempts and age, nest success, reproductive performance, and spring environment for female Black Brant (*Branta bernicla nigricans*) nesting colonially at the Tutakoke River, Alaska, 1987-1993. We observed little evidence of fidelity to natal sites, and young brant moved towards peripheral areas of the colony. Brant that showed no evidence of egg loss dispersed shorter distances than brant that experienced loss of eggs. Brant that initiated nests early dispersed farther than brant that initiated nests late. Neither nest success nor initiation date in year t+1 were related to dispersal distance (year t to year t+1), but clutch size declined with dispersal distance. Although generally not significant, annual variation (interaction) in the relationship between dispersal distance and measures of reproductive performance (i.e., initiation date and clutch size) suggest that this relationship may be influenced by weather conditions in spring. Evidence for the advantages of site fidelity in brant was equivocal. Dispersal distance explained little variation associated with

[1]Submitted to *Condor* as Lindberg, M.S., and J.S. Sedinger. Dynamics of nest-site fidelity in black brant.

reproductive performance. Variation in quality of individual birds, environmental conditions, and demographic status may be more important determinants of breeding performance in brant than potential benefits of site fidelity.

Key words: Alaska, Black Brant, Branta bernicla nigricans, *dispersal, fidelity, natal fidelity.*

INTRODUCTION

Ecological advantages of site familiarity have been proposed as a mechanism explaining evolution of philopatry in birds and other vertebrates (Lack 1954, Hinde 1956). Although fidelity to specific nest sites or nesting territories has been documented for a variety of avian species (see reviews by Greenwood 1980, Anderson et al. 1992), studies of ecological advantages of site fidelity are few because consequences of movement are rarely measured (Greenwood 1987). Instead, research has focused on correlation between reproductive success and probability of return to a breeding area or fidelity to a nest site (Greenwood and Harvey 1982). If reproductive success is site specific (Blancher and Robertson 1985), then birds that return to previously successful sites should be favored by natural selection (Gavin and Bollinger 1988). Nonetheless, a more direct assessment of factors important in the evolution of site fidelity would be a comparison of reproductive performance for faithful and dispersing individuals.

For female waterfowl, potential advantages of nest-site fidelity resulting from site fimiliarity may include improved nesting success, increased survival, improved feeding

efficiency, and higher brood-rearing success following hatching (Anderson et al. 1992). Although a number of waterfowl studies (e.g., Doty and Lee 1974, Majewski and Beszterda 1990) have demonstrated a correlation between nest success and probability of site fidelity, direct evidence for advantages of fidelity generally is lacking (Anderson et al. 1992). In 1 of the most extensive studies of site fidelity in waterfowl, Dow and Fredga (1983) observed earlier nesting, larger clutch sizes, and increased nest success for female Common Goldeneyes (*Bucephala clangula*) that exhibited fidelity to specific nest boxes. Gauthier (1990) reported similar findings for female Buffleheads (*Bucephala albeola*). Other studies detected no advantage to site fidelity (Hepp et al. 1989) or poorer reproductive performance (Hik 1986) by females faithful to nest sites. More rigorous tests of potential advantages of site fidelity in waterfowl are needed (Anderson et al. 1992). Furthermore, studies of the nest-site fidelity in waterfowl are generally limited to cavity-nesting species (Dow and Fredga 1983, Gauthier 1990) or species with well-defined nest structures (Doty and Lee 1974, Majewski and Beszterda 1990). Therefore, most studies have regarded fidelity as a discrete variable (i.e., faithful or not faithful to a specific nest site). Magnitude of dispersal effects, however, may increase as dispersal distance increases and familiarity with a new nesting location declines.

We tested for ecological advantages of nes- site fidelity in Black Brant, *Branta bernicla nigricans*, (hereafter brant) breeding at the Tutakoke River, Alaska. In contrast to most previous studies, we investigated potential advantages of site fidelity by examining the relationship between dispersal distance and breeding parameters. We therefore had a

direct assessment of the relationship between breeding performance and declining site familiarity. Like previous studies, we also examined factors affecting probability of fidelity. Specifically, we tested for relationships between demographic (age), reproductive (egg loss, nest initiation dates, and clutch size), and environmental (spring phenology) parameters and future fidelity to nest sites. Additionally, we used capture-recapture analysis to estimate probability of fidelity to natal sites.

STUDY AREA

Brant are small geese (ca. 1.0-1.5 kg) that nest in coastal areas of Alaska, eastern Russia, and western Arctic Canada (Sedinger et al. 1993). Our study area was the Tutakoke River colony (61°15'N, 165°37'W) on the Yukon-Kuskokwim River Delta of western Alaska (Fig. 1). Since 1986, number of brant nesting at Tutakoke has increased from approximately 1,100 pairs (Sedinger et al. 1993) to 6,000 pairs in 1992 (Anthony et al. 1995). The colony currently occupies about 6 km of coast bounded by the Kashunuk River to the north and diminishing densities of nesting brant to the south. Brant nest predominantly within 1 km of coastal mudflats and the colony is intersected by numerous tidal sloughs. The portion of the colony north of the Tutakoke River is characterized by islands of vegetation (largely *Carex ramenskii* and *Elymus arenarius*) surrounded by tidal mudflats, whereas south of the Tutakoke, meadows of predominantly *Carex ramenskii* are interspersed with numerous ponds and lakes. Habitat characteristics of this region are described in detail by Kincheloe and Stehn (1991).

For estimates of age-related fidelity and dispersal we divided the colony into

geographic strata. In earlier analyses (Lindberg et al. 1995), we defined 4 strata bounded by tidal sloughs and rivers. We maintained these definitions of strata for age-related estimates of fidelity. We did not mark (web tag) goslings in the southern-most portion of the Tutakoke colony (stratum D), however, and we therefore restricted our analysis to 3 strata (A, B, and C; Fig. 1). Stratum C was expanded slightly to include the southern limit of our web tagging.

METHODS

BANDING AND NEST SEARCHING

Since 1986, we captured brant at the Tutakoke colony during the adult molt (July) and marked both goslings and adults with individually coded 2.5 cm high tarsal tags (Sedinger et al. 1995). We observed marked, female brant during subsequent summers (May - July) and mapped their nest locations with a geographic information system (ARC/INFO) as described in Lindberg et al. (1995). We located nests of marked brant by flushing females from nests and reading their tags with binoculars or 15-60 x spotting scopes. During egg laying and incubation (mid-May to mid-June), we located nests by searching 50 m radius plots (n = 34 to 49). Plots were located in a stratified-random design throughout the breeding colony. We searched each plot every 4th day until egg laying was complete. Nests of marked females not on plots were located opportunistically while traveling between plots. During hatching (mid to late-June), when females are more tenacious to nest sites, we intensified our search effort by attempting to visit all nests on the colony at least every other day.

AGE RELATED MOVEMENT PROBABILITY

We used multistate modeling (Brownie et al. 1993) and program MSSURVIV (Hines 1994) to obtain estimates of fidelity (ψ_i^{rr}), dispersal (ψ_i^{rs}; hereafter collectively referred to as movement probability (ψ)), survival (S_i^r), and detection (p_i^s) probabilities. Program MSSURVIV is a modified version of program SURVIV (White 1983), which produces maximum likelihood estimates of parameters based on capture histories of individuals. Capture histories in MSSURVIV, however, include not only time of capture for marked individuals, but also the state or stratum of capture (Brownie et al. 1993). For example, the capture history for a marked brant observed nesting in stratum C at age *i*, not seen at age *i*+1, and observed nesting in stratum A at age *i*+2, is C0A. ψ_i^{rr} was defined as the probability of being in stratum *r* at age *i*+1 for brant that were in stratum *r* at age *i* and survived and returned to the Tutakoke colony at age *i*+1. ψ_i^{rs} was defined as the probability of being in stratum *s* at age *i*+1 for brant that were in stratum *r* at age *i* and survived and returned to the Tutakoke colony at age *i*+1. S_i^r was defined as the probability of being alive and returning to the Tutakoke colony at age *i*+1 for brant alive and in stratum *r* at age *i*, and p_i^s was defined as the probability of detection at age *i* for a bird in stratum s. Although we included age- and stratum-specificity in these parameters estimates, we were unable to consider year-specificity because we could not obtain meaningful estimates of all parameters with our sample sizes (Table 1). If age, strata, and year effects were all considered simultaneously, 171 movement probabilities would be

possible. By limiting our estimates to age- and strata-specificity we reduced the maximum number of movement probabilities to 45 (Table 1). Although elimination of year-specificity reduced parameter space, this assumption also affected our estimates of S_i^r. Our estimates of S_i^r were lower than true survival because of permanent emigration and right censoring of year cohorts. For example, estimates of S_i^r between ages 4 and 5 reflect mortality, permanent emigration, and censoring of the 1989, 1990, and 1991 cohorts (Table 1).

We used a step-down approach to obtain parameter estimates and test specific hypotheses (Lebreton et al. 1992). With this approach we first attempted to reduce the number of parameters in our models by constraining p_i^s and S_i^r equal over ages (p^s, S^r), strata (p_i, S_i), or both (p, S), while ψ remained both age- and stratum-specific. This approach reduced variance in estimates of the ψ and increased power for hypothesis tests about ψ (Lebreton et al. 1992). We considered 16 models that constrained p and S over ages and strata and selected the most parsimonious model that fit our data, based on Akaike information criteria (AIC, Akaike 1973), likelihood ratio tests (LRT) between nested models, and χ^2 goodness-of-fit tests (Brownie et al. 1993). After selecting this model, we maintained model constraints on p and S and considered models that constrained ψ and tested hypotheses regarding age and strata effects on ψ.

Our sample for estimates of natal movement was limited to brant webtagged in the nest as goslings (known natal site) that were subsequently captured during banding and marked with tarsal tags. These birds were tarsal tagged as goslings or during the next

summer; we have not observed brant nesting at Tutakoke until 2 years of age. Therefore, our estimates of natal movement were from natal nest sites to nest sites at age 2. We obtained a tagged sample of brant ages 2 to 5 from this sample, by recapturing previously web-tagged goslings >1 year old, or by tarsal tagging brant that were identified as 1-year-old birds based on plumage characteristics (Jones 1964). Our sample of known-age brant included birds banded between 1986 and 1991 that were subsequently observed nesting at Tutakoke between 1987 and 1993.

NEST SUCCESS AND MOVEMENT PATTERNS

Between 1988 and 1993, we digitized and calculated distances between nest sites of marked female brant nesting at Tutakoke River using ARC/INFO (Lindberg et al. 1995). We only estimated distances between sites for females observed nesting in consecutive years. Because some females were observed in more than 2 consecutive nesting attempts, we randomly selected 1 pair of observations for these females to avoid pseudoreplication in subsequent analysis.

We examined the relationship between nest fate in year t and dispersal distance between year t and year t+1, by comparing the distribution of dispersal distances for brant with nests that suffered no detectable reduction in clutch size (SUC) and brant with nests that suffered partial or complete loss of eggs (UNSUC). We determined fate of nests by labeling eggs with permanent markers when nests were initially discovered and recording loss of eggs during subsequent visits (Flint and Sedinger 1992). Potential causes of egg loss included predation, nest abandonment, flooding, and dead or addled eggs. Because

brant classified as SUC included some nests where we failed to detect an event that reduced clutch size, our test of differences in dispersal distances between SUC and UNSUC brant was conservative. We tested for among-year variation in dispersal distances within SUC and UNSUC groups with Kruskal-Wallis tests (PROC NPAR1WAY, SAS Inst. Inc. 1990). We tested the hypothesis that median dispersal distance for SUC brant was different from UNSUC brant with randomization tests (Manly 1991).

To examine the relationship between dispersal distance and nest fate, we compared nest fate in year t+1 and dispersal distance between year t and year t+1. Nest fate was defined previously (i.e., SUC and UNSUC). We used Kruskal-Wallis tests to examine among-year differences in dispersal distances and randomization tests for differences in median dispersal distances (year t to year t+1) for SUC and UNSUC brant in year t+1. We could not specifically test for age effects or an interaction between age and nest success in either of the analysis described above because few brant in our sample were of known age. We minimized the effects of age by limiting our samples to females >2 years old in year t.

REPRODUCTIVE PERFORMANCE AND DISPERSAL PATTERNS

Previous studies of site fidelity have used a variety of measures of reproduction to examine the relationship between reproductive performance and site fidelity. Clutch size is a common measure of reproductive performance in birds, so we examined the relationship between dispersal distance and clutch size. We also examined the relationship

between initiation date and dispersal distance, because in brant, both clutch size (Flint and Sedinger 1992) and subsequent growth and development of goslings (Sedinger and Flint 1991), are correlated with initiation date. If poor reproductive performance results in greater dispersal distance, then we would expect brant with later initiation dates and smaller clutches to disperse farther. Conversely, if greater dispersal distance reduces site familiarity, and therefore reproductive performance, then brant dispersing farther should have later initiation dates and smaller clutches.

Initiation date was defined as the day the first egg was laid, and for nests located during laying was calculated by assuming 1 egg was laid each day, or by backdating from hatching date for nests observed after laying. Clutch size was defined as the maximum number of eggs observed in a nest. Our sample of clutches included nests located during laying and incubation. We eliminated nests with >6 eggs because these clutches may result from parasitic laying (Flint and Sedinger 1992). To avoid pseudoreplication, we again randomly selected 1 pair of observations for females that were observed more than once. We reduced effects of age by limiting our sample to females >2 years of age in year *t*. We removed the effects of nest fate on dispersal distance by excluding females that were UNSUC nesters in year *t* from our sample.

We used ANCOVA (PROC GLM, SAS Inst. Inc. 1990) to test for a relationship between reproductive performance and dispersal distance. Dispersal distance between year *t* and year *t*+1 was the dependent variable, year *t* and clutch size in year *t* were fixed factors, and initiation date in year *t* was the covariate in the analysis that examined effects

of reproductive performance on dispersal distance. In the ANCOVAs comparing dispersal distance and resulting reproductive performance, year t+1 was the fixed factor, dispersal distance between year t and year t+1 was the covariate, and either initiation date in year t+1 or clutch size in year t+1 was the dependent variable. Initiation date in year t+1 was included as a covariate in the later model.

Relationship between reproductive performance and dispersal distance was complicated by variation in spring phenology. Phenology of spring snowmelt affects initiation dates and clutch size (Lindberg et al. unpubl. data) and also may be correlated with dispersal distance (Abraham 1980). The date on which the study area was 100% snow free ranged from 17 May to 2 June between 1988 and 1993. We categorized 1989 and 1992, which were 100% snow free between 28 May and 2 June, as late years. All remaining years (1988, 1990, 1991, and 1993) were considered early because 100% snowmelt occurred between 17 May and 21 May. We investigated effects of spring snowmelt on the relationship between dispersal distance and reproductive performance of brant by including interaction terms in ANCOVA models described previously. Specifically, we tested if the relationship between initiation date and dispersal distance (initiation date*year interaction), clutch size and dispersal distance (clutch size*year), and dispersal distance and reproductive performance (dispersal distance*year) varied by year.

REPEATABILITY

Repeatability among individuals provides a maximum estimate of heritability by estimating the amount of variance in a character resulting from among-, rather than within-individual

variation (Falconer 1989). We obtained estimates of among-individual repeatability (Lessels and Boag 1987) of dispersal distance for adult female brant nesting at Tutakoke using individuals for which we had measured distances between consecutive nesting attempts on at least 2 occasions between 1988 and 1993. We estimated standard error of repeatability following Becker (1984).

RESULTS

AGE RELATED MOVEMENT PROBABILITY

From 1987 to 1993, we recorded nesting strata of 551 marked females of known age, totalling 782 observations. We determined natal-nesting strata of 371 of these females. Natal dispersal distances averaged 1,316 m ($n = 11$, $\widehat{SE} = 320$ m) between natal nest sites and the nest site first detected when these birds were 2 or 3 years old. This sample was small because not all nest sites were mapped (digitized) even though nesting strata were recorded.

Of the 16 MSSURVIV models that constrained p_i^r and S_i^r over ages and strata, the model with the lowest AIC value (277) was a model with age-specific p_i and S_i ($p_i S_i \psi_i^{rs}$). Therefore, we adopted these model constraints and tested for age and stratum effects on ψ. We tested if all ψ were equally probable by constraining all ψ to 0.33 (model $p_i S_i \psi_{0.33}$). Based on AIC values and the LRT between this model (model $p_i S_i \psi_{0.33}$) and the more general model with age and stratum specific ψ ($p_i S_i \psi_i^{rs}$), we rejected ($\chi^2 = 369.5$, df = 30, $P < 0.001$) the hypothesis of equally probable movement among strata (Fig. 2). We therefore constrained fidelity (ψ_i^{rr}) and dispersal (ψ_i^{rs}) probabilities separately

for subsequent tests.

We considered 2 groups of models (Fig. 2); for the first group, we removed strata differences in ψ_i^{rr} and ψ_i^{rs}, and then progressively removed age effects within ψ_i^{rr} and ψ_i^{rs} by equating 4 and 5 year olds (model $\psi_{45}^{s}\psi_{45}^{r}$); then 3, 4 , and 5 year olds equal (model $\psi_{35}^{s}\psi_{35}^{r}$), until all age classes were equal (model $\psi_{15}^{s}\psi_{15}^{r}$). For the second group of models we maintained strata specificity in ψ_i^{rr} and ψ_i^{rs} and again progressively removed age effects (models $\psi_{45}^{rs}\psi_{45}^{rr}$ through $\psi_{15}^{rs}\psi_{15}^{rr}$).

Based on AIC and LRT, models that maintained strata-specific ψ were selected over the more general model ($p_t S_t \psi_i^{rs}$); however, these models generally had AIC values higher than the group of models that removed strata specificity (Fig. 2). Model $\psi_{45}^{s}\psi_{45}^{r}$ had the lowest AIC value (248) in the group without strata specificity and was also selected over other models in this group based on LRT. We therefore concluded that neither ψ_i^{rr} nor ψ_i^{rs} were strata-specific and both parameters were equal for 4 and 5 year olds.

Finally, we tested if all natal movements were equally probable by comparing model $\psi_{45}^{s}\psi_{45}^{r}$ to a model ($\psi_{45}^{s}N\psi_{45}^{r}N$) with identical constraints except that all natal ψ were constrained to equal 0.33. The AIC for model $\psi_{45}^{s}N\psi_{45}^{r}N$ was 255 and the LRT between models rejected ($\chi^2 = 10.9$, df = 2, $P = 0.004$) the hypothesis of equally probable natal ψ. We therefore used model $\psi_{45}^{s}\psi_{45}^{r}$ to obtain parameter estimates.

With program MSSURVIV, only n-1 of the ψ per strata were estimated directly (Brownie et al. 1993). Therefore, one ψ per strata was estimated by subtraction (Hines 1994). For our analysis, ψ s to stratum A (i.e., ψ_i^{AA} , ψ_i^{BA} , and ψ_i^{CA}) were obtained by

subtraction. When we examined parameter estimates under model $\psi^{s}_{45}\psi^{r}_{45}$, we noticed ψ^{AA}_{i} > $\psi^{BB}_{i} = \psi^{CC}_{i}$, and both ψ^{BA}_{i} and ψ^{CA}_{i} were higher than all remaining ψ^{rs}_{i}. We were concerned that these differences were an artifact of our model design because all ψ^{rr}_{i} were never directly compared and ψ^{BA}_{i} and ψ^{CA}_{i} were never compared to other ψ^{rs}_{i}. Therefore, we maintained model $\psi^{s}_{45}\psi^{r}_{45}$ constraints, but designed the model (i.e., we changed the flag to 0; Hines 1994) so all ψ^{rr}_{i} were obtained by subtraction and all ψ^{rs}_{i} were directly estimated (model $\psi^{s}_{45}0\psi^{r}_{45}0$). The AIC for model $\psi^{s}_{45}0\psi^{r}_{45}0$ was 254 and we again rejected the hypothesis that all ψ^{rs}_{i} and ψ^{rr}_{i} were equal. We therefore concluded that ψ^{AA}_{i} > ψ^{BB}_{i} = ψ^{CC}_{i}, and that ψ^{BA}_{i} and ψ^{CA}_{i} were greater than all remaining ψ^{rs}_{i}.

Under model $\psi^{s}_{45}\psi^{r}_{45}$, ψ^{rr}_{i} increased with age for all strata and was equal to 1.00 ($\widehat{SE}$ < 0.13) for 4 and 5 year old brant (Fig. 3). ψ^{rs}_{i} were directional (i.e., towards strata A) before stabilizing at age 4. Natal ψ^{rr}_{i} ranged from 0.72 ($\widehat{SE}$ = 0.10) for stratum A to 0.35 ($\widehat{SE}$ = 0.12) for strata B and C. $\hat{p}_{i}$ increased from 0.27 ($\widehat{SE}$ = 0.07) for 2 year olds to 0.64 ($\widehat{SE}$ = 0.09) for 5 year old brant. $\hat{S}_{i}$ from 0 to 2 year old was 0.14 ($\widehat{SE}$ = 0.02) and $\hat{S}_{i}$ increased to 0.77 ($\widehat{SE}$ = 0.07) for 2 year old brant. $\hat{S}$ declined (e.g., $\hat{S}_{i}$ = 0.63, $\widehat{SE}$ = 0.09, for ages 4 to 5) with age as cohorts were progressively removed from the sampling design (Table 1).

NESTING SUCCESS AND MOVEMENT PATTERNS

Distribution of dispersal distances was highly skewed (Figs. 4 and 5). Ranks of dispersal distances (year *t* to year *t*+1) did not differ among years for brant that were SUC (χ^2 = 9.35, df = 4, P = 0.05) or UNSUC (χ^2 = 0.33, df = 3, P = 0.95) in year *t*. We therefore

pooled data across years for subsequent analysis. Brant that were UNSUC in year t dispersed farther ($P = 0.026$, $n = 5{,}000$) between year t and year $t+1$ than brant that were SUC in year t (Fig. 4). Median dispersal distance (year t to year $t+1$) was 110m ($n = 268$) and 171 m ($n = 74$) for SUC and UNSUC brant, respectively.

We failed to observe annual variation in ranks of dispersal distances between year t and year $t+1$ for brant that were SUC ($\chi^2 = 9.21$, df = 4, $P = 0.06$) or UNSUC ($\chi^2 = 5.59$, df = 4, $P = 0.23$) in year $t+1$. Therefore data were pooled across years. Nest fate (year $t+1$) was not related to dispersal distance (year t to year $t+1$) as we failed to detect a difference ($P = 0.646$, $n = 5{,}000$) between median dispersal distance (year t to year $t+1$) for SUC (139 m, $n = 251$) and UNSUC (130 m, $n = 84$) brant (Fig. 5).

REPRODUCTIVE PERFORMANCE AND MOVEMENT PATTERNS

Effects of Reproductive Performance on Dispersal Distance. Examination of residual and normal scores plots from analysis of effects of initiation date and clutch size in year t on dispersal distance between year t and year $t+1$ revealed that dispersal distances were skewed and that error variance was not constant (heteroscedasticity). We therefore performed a natural-log transformation on dispersal distances, which stabilized error variance and improved normality, and conducted analyses on transformed distances.

We observed no difference ($F_{4,189} = 1.03$, $P = 0.395$) in ln(dispersal distance) among years. Neither clutch size ($F_{4,189} = 0.13$, $P = 0.971$) or initiation date ($F_{4,189} = 0.44$, $P = 0.510$) in year t was significantly related to ln(dispersal distance) between year t and year $t+1$ and this relationship did not vary among years (year*initiation date interaction,

$F_{4,189} = 0.98$, $P = 0.417$; year*clutch size interaction, $F_{11,189} = 1.67$, $P = 0.081$). After the interaction terms were removed from the model, year ($F_{4,204} = 0.56$, $P = 0.693$) and clutch-size effects ($F_{4,204} = 0.29$, $P = 0.882$) remained nonsignificant, but we observed a significant ($F_{1,204} = 4.94$, $P = 0.027$) negative relationship between initiation date in year t and ln(dispersal distance) between year t and year t+1.

Effects of Dispersal Distance on Reproductive Performance. Although initiation dates varied among years ($F_{4,259} = 98.9$, $P < 0.001$), we noted no relationship ($F_{1,259} = 0.02$, $P = 0.875$) between dispersal distance (year t to year t+1) and initiation date in year t+1, and no significant ($F_{4,259} = 1.29$, $P = 0.273$) interaction in the full ANCOVA model (Fig. 6). These results were largely unchanged after the interaction term was removed ($F_{4,263} = 133.5$, $P < 0.001$- year effect, $F_{1,263} = 0.03$, $P = 0.872$ - distance effect). Analysis of influential points using Cook's distance measure, however, revealed 1 observation in both 1991 and 1992 that exceeded the 50th percentile of the corresponding F distribution (Neter et al. 1985). These observations are not surprising considering the highly leptokurtic distribution of dispersal distances. Therefore, we performed the ANCOVA after removing these points. Again we noted significant variation in initiation dates among years ($F_{4,257} = 93.18$, $P < 0.001$). Both distance ($F_{1,257} = 1.26$, $P = 0.264$) and interaction ($F_{4,257} = 0.94$, $P = 0.444$) effects remained nonsignificant (Fig. 6).

Clutch size in year t+1 varied significantly ($F_{4,241} = 2.88$, $P = 0.023$) among years and clutch size declined with dispersal distance (year t to year t+1) ($F_{1,241} = 3.96$, $P = 0.048$) and initiation date (year t+1) ($F_{1,241} = 13.6$, $P < 0.001$) (Table 2). We observed no

significant ($F_{4,241} = 1.26$, $P = 0.287$) interaction between dispersal distance and year. The interaction between initiation date and year however, was significant ($F_{4,241} = 2.87$, $P = 0.024$).

Effects of Spring Breakup Patterns. Although only 1 interaction term was significant in models describing the relationship between reproductive performance and dispersal distance, we observed 2 trends in reproductive performance relative to spring phenology. The negative relationship between dispersal distance and initiation date (year t+1) was strongest in late years (1989 and 1992) (Fig. 6). That is, brant nesting early in late years generally had dispersed farther the preceding year. Conversely, declines in clutch size (year t+1) with increasing dispersal distance were more prevalent in late years (Table 2).

REPEATABILITY

Between 1988 and 1993 we measured distance between consecutive nests attempts on >1 occasion for 104 females totaling 242 distances. Estimated repeatability of dispersal distance was 0.47 ($\hat{SE}$ = 0.07) (Table 3); repeatability was significantly ($P < 0.05$) different from 0.

DISCUSSION

AGE RELATED PROBABILITY OF MOVEMENT

Natal-site dispersal was strongly directional for brant females that returned to the Tutakoke River colony. Goslings hatched in all 3 strata were more likely to nest in stratum A as 2-year-olds than any other strata. Based on the social behavior of brant we

anticipated a low probability of fidelity to natal nest sites. Precocial young are brooded at the nest for a maximum of 48 hr before departure to brood rearing areas (Afton and Paulis 1992). During brood rearing, mixing of goslings from different families is common (Flint et al. 1995) and goslings may associate with nonbiological parents before fledging. Unlike many goose species, which maintain family integrity until return to the breeding grounds the following summer (Owen 1980), family disintegration has been observed in brant as early as fall staging (Jones and Jones 1966). Brant goslings therefore have little opportunity for site recognition. Finally, competition for nest sites, which results from colonial nesting (Welsh 1988) and earlier nesting by older birds (Finney and Cooke 1978, Flint and Sedinger 1992), may force birds to initially nest in peripheral areas of the colony (Kharitonov and Siegel-Causey 1988).

Although a number of studies have estimated return rates of female waterfowl to natal breeding areas (Rohwer and Anderson 1988, Anderson et al. 1992), few studies have investigated settlement pattern of females relative to natal nest sites. Based on 17 individuals that returned to their study area, Dow and Fredga (1983) suggested that female Common Goldeneyes nested in proximity to natal nest boxes. Coleman and Minton (1979) observed that female Mute Swans (*Cygnus olor*) generally breed within 8 km of their natal nest site, and Lessels (1985) suggested that female Canada Geese (*Branta canadensis*) breed in areas where they were banded as goslings. Hepp et al. (1989) reported that female Wood Ducks (*Aix sponsa*) generally dispersed short distances from natal wetlands. Although most nonwaterfowl species exhibit male-biased philopatry

to breeding areas, those females that do return tend to nest in proximity to natal sites (Greenwood 1980, Greenwood and Harvey 1982).

Unlike some colonial nesting seabirds (Kharitonov and Siegel-Causey 1988), which attempt to establish territories in the center of the colony in later breeding attempts, we observed an increase in nest-site fidelity with age indicating that brant tend to breed in the same area following initial nesting. Lesser Snow Geese (*Chen caerulescens caerulescens*) nesting at La Perouse Bay, Manitoba exhibited a similar pattern of site fidelity (Cooke et al. 1983). Cooke et al. (1983) further demonstrated that Lesser Snow Geese exhibited a pattern of cohort settlement in which geese of similar age nest in proximity to one another. The strong directional movements we observed over 5 years suggest the potential for cohort affiliations in brant. We observed little evidence that these cohorts associated with natal areas.

In 1992 and 1993, nest densities in stratum A exceeded densities in all other strata. Natal movement therefore altered the nesting distribution of brant at Tutakoke as stratum A was nearly vacant in 1985. We expect patterns of natal dispersal for future recruits will change if nest densities and competition for available nest sites continues to increase in stratum A. Our results indicate that natal dispersal is a mechanism for colony expansion in brant. During the 1960's the Tutakoke colony ranged approximately 5 km farther north along the banks of the Kashunuk River (Shepard 1964, Sedinger et al. 1993). We suspect that these areas may be reoccupied if current levels of recruitment are maintained and suitable nesting habitat exists. Alternatively, nest densities in stratum C of the Tutakoke

colony have continually declined since the current study was initiated in 1984 and future recruits may reoccupy these areas as densities decline as a result of mortality in older birds.

Dispersal from natal sites has been proposed as a mechanism for inbreeding avoidance (Greenwood 1987). Even if female brant nested in close proximity to natal sites, inbreeding would still be unlikely. Black brant, like most waterfowl species, exhibit a pattern of male-biased dispersal from breeding areas (Anderson et al. 1992) and pair formation generally occurs on wintering grounds (Rohwer and Anderson 1988, McKinney 1992).

DOES NEST FATE OR REPRODUCTIVE PERFORMANCE AFFECT SITE FIDELITY?

We observed an increase in dispersal distance for female brant that experienced a reduction in clutch size. As described in other studies of waterfowl (Doty and Lee 1974, Dow and Fredga 1983, Gauthier 1990, Majewski and Beszterda 1990, Lokemoen et al. 1990) and nonwaterfowl (Greenwood et al. 1979, Harvey et al. 1979, Burger 1982, Newton and Marquiss 1982, Drilling and Thompson 1988, Gavin and Bollinger 1988), nest fate was an important determinant of future site fidelity.

Dow and Fredga (1983) suggested that increased dispersal distance by unsuccessful nesters is an adaptive strategy to avoid repeated nest depredation by predators with established territories. Burger (1982) demonstrated that Black Skimmers (*Rynchops niger*) were more likely to abandon colonies destroyed by predators than colonies destroyed by flooding. Similarly, Gavin and Bollinger (1988) suggested that nest

failure resulting from predation was the most important factor for predicting probability of fidelity for Bobolinks (*Dolichonyx oryzivorus*). During our study, Arctic foxes (*Alopex lagopus*), the major nest predator of brant on our study area, were removed and fox predation was minimal compared with years preceding our study (Anthony et al. 1991). Of the 74 nests classified as UNSUC, 76% (n = 56) were identified based exclusively on the presence of dead or addled eggs in the nests. Only 13 nests (18%) showed evidence of predation by Arctic foxes, Glaucous Gulls (*Larus hyperboreus*), or flooding, and 6 nests experienced total loss of the clutch. Predation therefore was not the only form of nest failure related to movement patterns of brant. Small sample sizes, however, precluded testing if dispersal distances would be greater for nests destroyed by predators.

Brant that initiated nests earlier had greater dispersal distances (Fig. 6), but we observed no relationship between clutch size and dispersal distance. This result was not expected because brant that nest early lay larger clutches (Flint and Sedinger 1992) and produce larger goslings that grow faster (Sedinger and Flint 1991) than brant that initiate nesting later. In addition, other studies indicate that higher reproductive performance at a nest site results in lower dispersal probability (Harvey et al. 1979, Blancher and Robertson 1985, Drilling and Thompson 1988, Gavin and Bollinger 1988) . Why then, would brant disperse from nest sites that apparently afford early initiation dates? This pattern might be explained by lower nesting success for brant nesting early, as was observed for Barnacle Geese (*Branta leucopsis*) (Prop and de Vries 1993), but we restricted our sample for analysis of the relationship between initiation date and dispersal distance to nests with no

detectable loss of eggs. We would also expect a decline in dispersal distance with later initiation date if younger brant nested earlier. Two-year-old brant nest later than older brant (Flint and Sedinger 1992), and we suspect that older brant generally nest earlier, as reported in Lesser Snow Geese (Finney and Cooke 1978). In addition, we reduced age-related variation in our analysis by restricting our sample to females >2 years old in year *t*.

Earlier analysis (Lindberg et al. 1995) indicated that brant moving >200 m from a previous nest site had a lower probability of remaining at the new nest site than those individuals that remained within 200 m of their previous nest site. We suspect that brant may disperse from nest sites to achieve early initiation dates, particularly in late years. Hence, greater dispersal distance by brant nesting earlier may reflect movement from new nest sites or return to previous nest sites.

IS SITE FIDELITY ADVANTAGEOUS?

We observed no evidence that dispersal distance increased probability of egg loss (Fig. 5). Our findings are in contrast to Dow and Fredga (1983), who reported lower nesting success for female Goldeneyes that moved to new nest boxes. Hik (1986), however, reported lower hatching success and higher rates of gosling abandonment for Lesser Snow Geese faithful to nesting areas. Unlike cavity-nesting species (Dow and Fredga 1983, Gauthier 1990), for which nesting success may be related to characteristics of the nest location (Savard 1985, Blancher and Robertson 1985), habitat characteristics of nest sites for brant show little variation among locations. Brant nesting in higher densities may delay or retard predation by Arctic foxes through predator swamping (Raveling 1989),

but, except for nests sites on islands (Sedinger pers. obs) predation rates do not appear to vary across habitat types (Stickney 1989). Between 1988 and 1993 only 21% (n = 5,300) of nests at Tutakoke were located on islands and a proportion of these island sites were located in ponds with shallow water (<50 cm) or ephemeral ponds. Nest success at Tutakoke was 2% in 1984 and 7% in 1985 indicating that few nests sites were protected from fox predation (Anthony et al. 1991). Therefore, we do not believe nest success would be higher for brant faithful to nest sites even in years with higher rates of predation by Arctic foxes.

Nest-intiation date was not positively related to dispersal distance of brant. Indeed, in late years, brant that dispersed tended to nest earlier (Fig. 6). Several studies have observed earlier nesting by waterfowl that return to nest sites than for individuals that dispersed to new sites (Dow and Fredga 1983, Gauthier 1990, MacInnes and Dunn 1988). Newton and Marquiss (1982) suggested that sparrowhawks (*Accipter niscus*) may experience a tradeoff between fidelity and local food supplies. Similarly, we believe a tradeoff between site fidelity and timing of nest initiation may explain the relationship we observed. We hypothesize that dispersal from nest sites is a strategy to nest earlier than would otherwise be possible in late years.

Timing of nest initiation is important for subsequent reproductive performance of brant (Sedinger and Flint 1991) and other species breeding at high latitudes (e.g., Cooch et al. 1991). Nesting chronology, particularly for Arctic nesting geese, is closely regulated by phenology of spring breakup (Raveling 1978). Date of nest initiation at Tutakoke

River vary among years relative to spring snowmelt, and earliest nesting brant use highest-elevation nest sites (Lindberg et al. unpubl. data). If nest sites are not available when brant arrive on breeding grounds, geese may delay breeding until sites become available (Raveling 1978), lay their eggs in the nests of other geese (dump-nesting, e.g., MacInnes and Dunn 1988), abandon breeding for that year, or disperse to available nest sites (Abraham 1980). We observed little evidence of long delays between arrival and nest initiation (Raveling 1978) or dump nesting (Lindberg et al. unpubl. data) by brant in late springs. Estimates of breeding propensity are approximately 1.00 for brant >5 years old (Sedinger et al. unpubl data). Even if some individuals abandon nesting in late years, our current analysis indicates that some brant breeding in late years disperse to available nest sites. Selective pressures for early nesting associated with increased growth and development of goslings may be greater in late years (Cooch et al. 1991). We suggest that brant do not delay breeding to maintain fidelity in these years. Rather, brant nesting early in late springs (year t+1) generally dispersed farther between year t and year t+1 than brant nesting later (Fig. 6). Brant dispersing 1,000 m in late springs advanced their initiation date by approximately 1.3 days. Reduced availability of nests sites caused by meltwater flooding (Lindberg unpubl. data) and heightened competition for fewer nest sites (Barry 1962) are likely causes of these dispersal patterns. We lack data on variation in timing of availability of all nests, but even in late years traditional nest sites of some individuals were available immediately upon arrival. Some brant moving <100 m in late years nested as early as those brant moving >1,000 m (e.g., 1992 Fig. 6) probably because

they acquired higher elevation nests.

Clutch size in brant declined with dispersal distance, particularly in late years (Table 3). Dow and Fredga (1983) and Gauthier (1990) demonstrated that birds returning to nest boxes had larger clutches than individuals moving to new nests boxes. This increase in clutch size may reflect a relationship between date of nest initiation and clutch size (Klomp 1970) because birds faithful to nest boxes nested earlier in both studies (Dow and Fredga 1983, Gauthier 1990). Furthermore, Dow and Fredga (1983) failed to observe a relationship between dispersal distance and clutch size. Fidelity to nest sites may reduce time spent searching for new nest sites and increase familiarity with local resources (Lack 1954, Hinde 1956), thereby reducing expenditure of nutrient reserves devoted to egg production (Raveling 1978, Alisaukas and Ankney 1992).

Alternatively, lower clutch size may not result from dispersal, but instead may reflect variation in quality of individual brant. We could not determine if brant would have laid larger clutches if they had maintained fidelity to previous nest sites. If competition for available nest sites is heightened in late years (Barry 1962), we suspect that lower-quality individuals or small-clutch phenotypes may be more likely to disperse.

We could not experimentally distinguish effects of dispersal, per se, from those resulting from individual quality. We noted little evidence, however, to suggest fidelity to nest sites was advantageous. Despite several theoretical explanations for ecological advantages of site fidelity (Lack 1954, Greenwood and Harvey 1982, Anderson et al. 1992), little empirical evidence is available to test these hypotheses. During nesting, brant

frequently fly to coastal areas to feed rather than feeding in the immediate vicinity of nest sites (Welsh 1988) . Therefore, familiarity with local food resources may not be enhanced by fidelity to specific nest sites. Benefits of site fidelity may be realized at other geographic scales (i.e., philopatry to colonies) or during periods of the breeding cycle (e.g., brood rearing) when familiarity with available food is more important (i.e., brood rearing) (but see Cooch et al. 1993).

Dispersal distance may be an additional factor affecting reproductive strategies of individuals (Drent and Daan 1980) because brant that dispersed nested early, but laid smaller clutches than those individuals faithful to nest sites. Our estimate of repeatability indicate that dispersal strategies may have some genetic basis; however, these estimates may be biased by return of females to traditional nest sites following dispersal as well as other sources noted by van Noordwijk (1987). We suggest that environmental effects, age, and nest fate are more important parameters affecting movement patterns of brant.

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TABLE 1. Sampling protocol used to estimate age-specific movement probabilities of Black Brant nesting at the Tutakoke River colony, Alaska, 1987-1993. For each cohort, 0 indicates that the cohort was not used to estimate a parameter, whereas cells filled with a parameter show what parameter was estimated.

	Age				
Cohort	0-2	2-3	3-4	4-5	5-6
1986	0	Ψ_2	Ψ_3	Ψ_4	Ψ_5
1987	Ψ_1	Ψ_2	Ψ_3	Ψ_4	Ψ_5
1988	Ψ_1	Ψ_2	Ψ_3	Ψ_4	0
1989	Ψ_1	Ψ_2	Ψ_3	0	0
1990	Ψ_1	Ψ_2	0	0	0
1991	Ψ_1	0	0	0	0

TABLE 2. Regression parameters for the relationship between clutch size in year t+1, initiation date in year t+1, and dispersal distance between year t and year t+1 for brant nesting at Tutakoke River, Alaska, 1988-1993.

Year	β_{ID}[a]	β_{DD}[b]	n
1989	-0.3548	-0.00122	9
1990	-0.0864	0.00003	25
1991	-0.2429	-0.00003	51
1992	-0.1693	-0.00023	64
1993	-0.2429	-0.00001	107

[a] Estimated slope of relationship between clutch size and initiation date.

[b] Estimated slope of relationship between clutch size and dispersal distance.

TABLE 3. ANOVA table values used to estimate repeatability of dispersal distances for adult female brant nesting at Tutakoke River, Alaska from 1988 to 1993.

Source	df	SS	MS	F	*P*
Among Individuals	103	80829800	784755	3.06	0.0001
Within Individuals	138	35436469	256786		
Total	241	116266269			

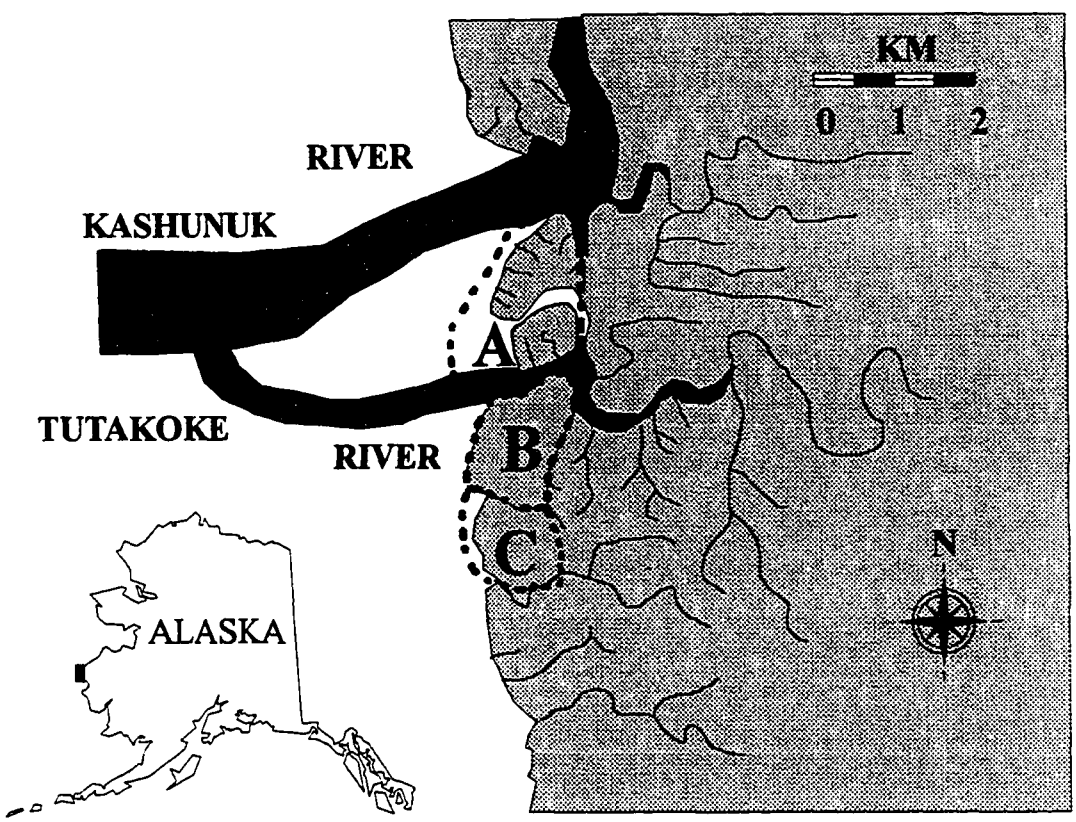

FIGURE 1. Location of the Tutakoke River Black Brant colony on the Yukon-Kuskokwim River Delta, Alaska. Tidal sloughs are shown with thin black lines and strata boundaries are shown with dashed lines.

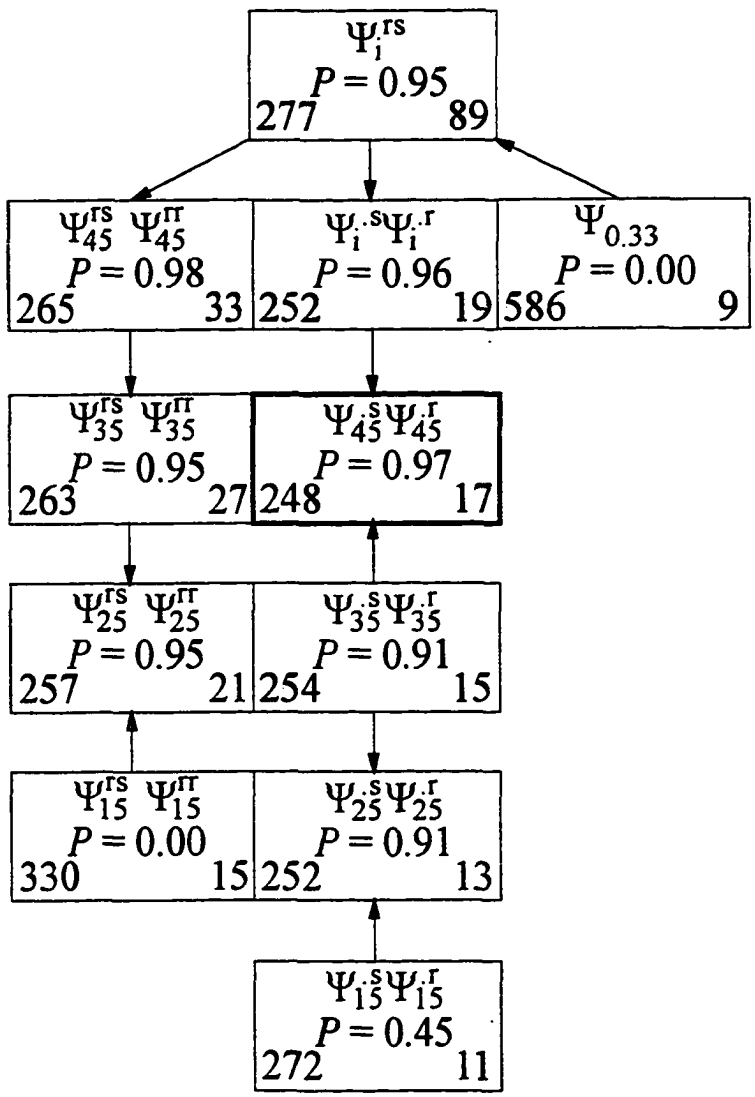

FIGURE 2. Diagram of hierarchy used to select model for estimates of age related movement probabilities of Black Brant. Model names are shown at top of box, *P*-values for χ^2 goodness-of-fit tests in the center of the box, AIC values in the lower left corner, and number of parameters in the model in the lower right corner. Arrows between boxes point to model selected based on likelihood ratio tests between nested models. Bolded box highlights model selectedbased on AIC and LRT.

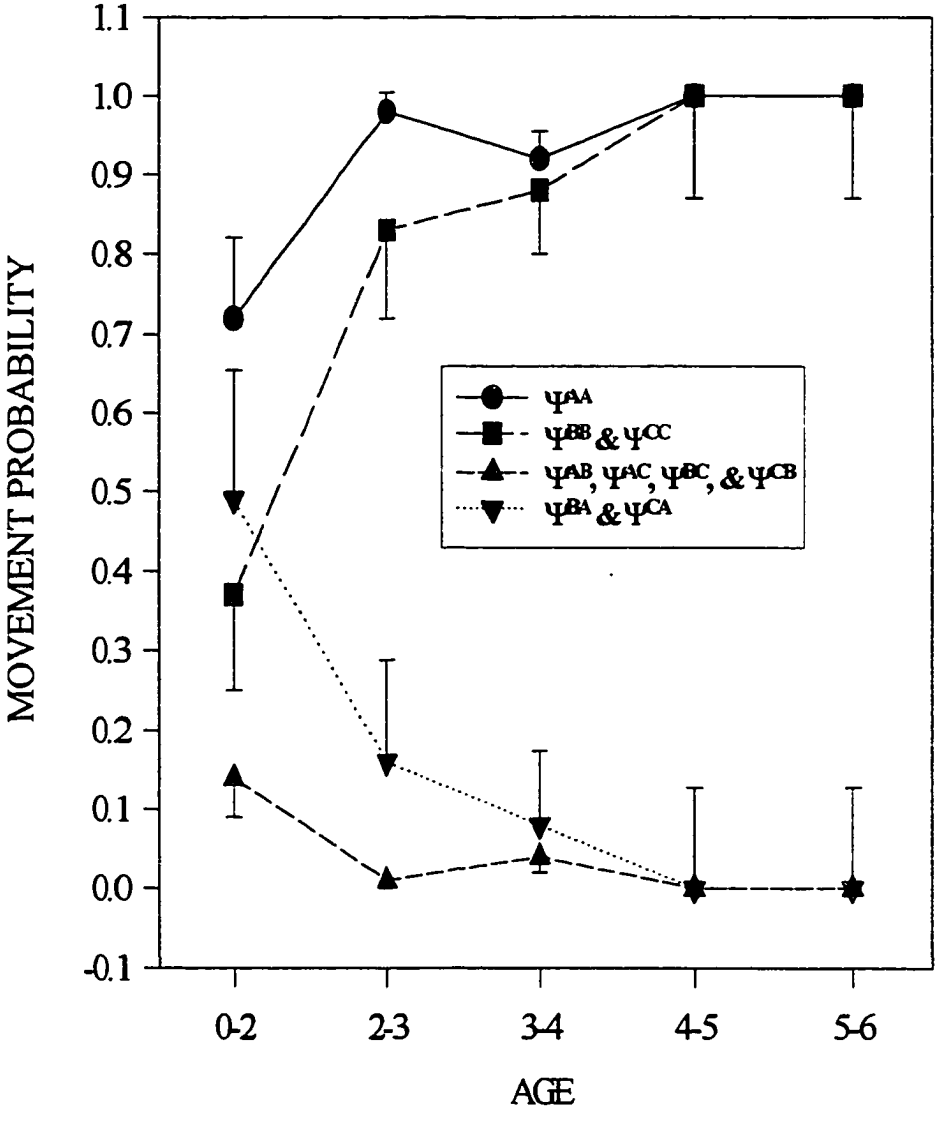

FIGURE 3. Estimates of age related fidelity (Ψ^{m}) and dispersal (Ψ^{m}) probabilities among strata (A, B, and C) for Black Brant breeding at Tutakoke River, Alaska, 1987-1993. Error bars represent 1 standard error.

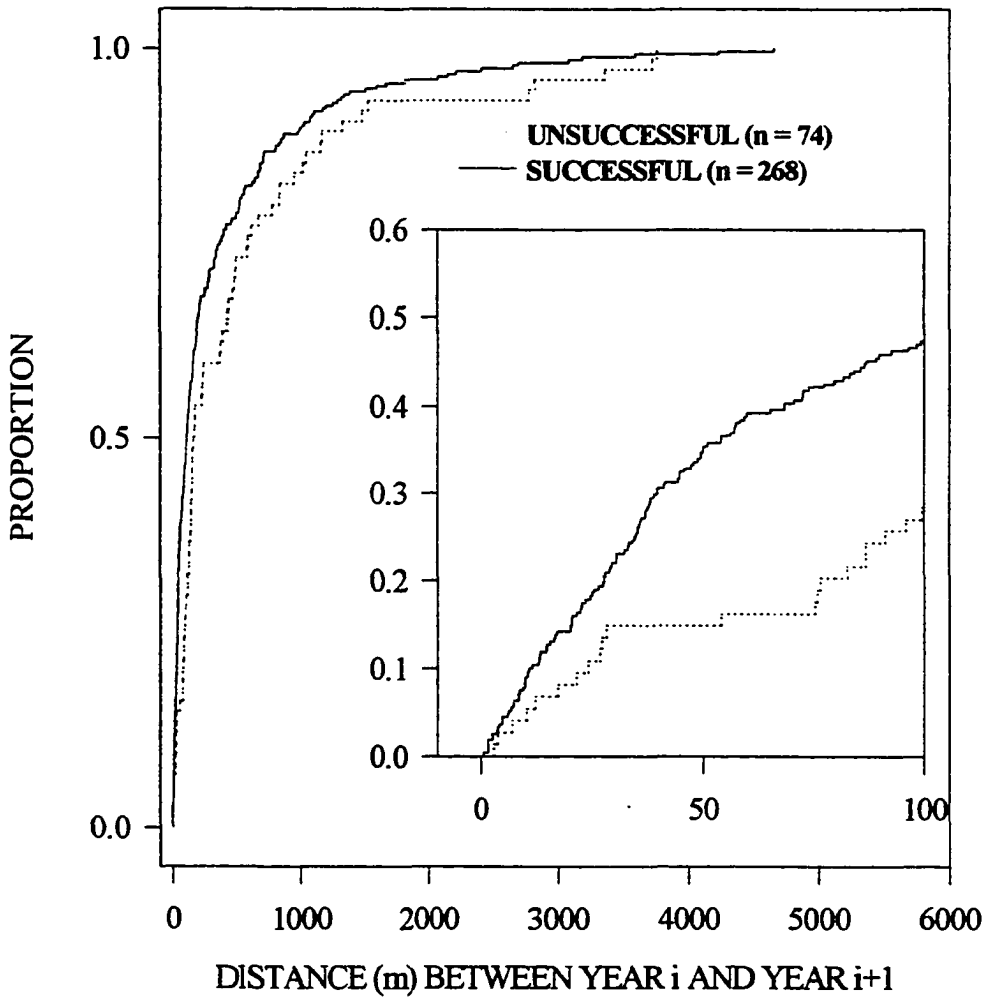

FIGURE 4. Distribution of dispersal distances (year *t* to year *t*+1) between consecutive nesting attempts for successful and unsuccessful (year *t*) Black Brant at the Tutakoke River, Alaska, 1988-1993. Successful nests were those with no detectable loss of eggs and unsuccessful nests had at least 1 egg that did not hatch. Insert shows proportions between 0 and 100 m.

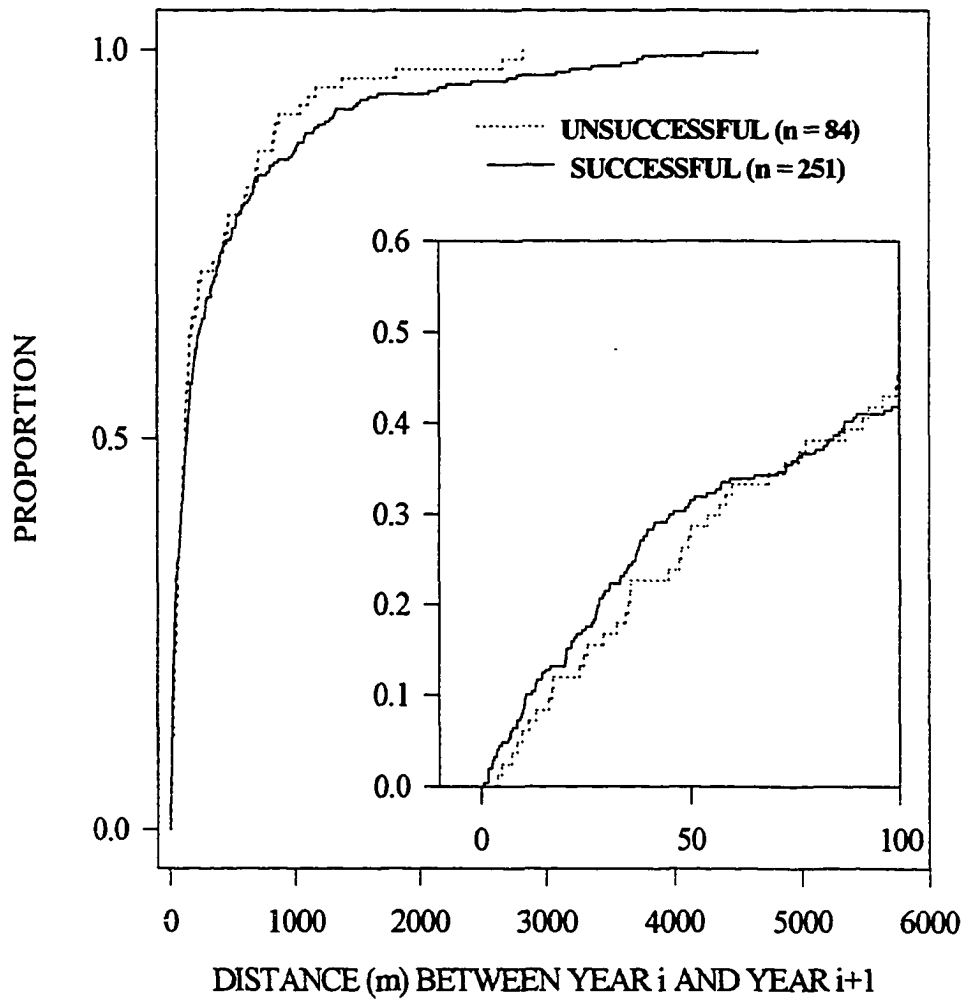

FIGURE 5. Distribution of dispersal distances (year *t* to year *t*+1) between consecutive nesting attempts for successful and unsuccessful (year *t*+1) Black Brant at the Tutakoke River, Alaska, 1988-1993. Successful nests were those with no detectable loss of eggs and unsuccessful nests had at least 1 egg that did not hatch. Insert shows proportions between 0 and 100 m.

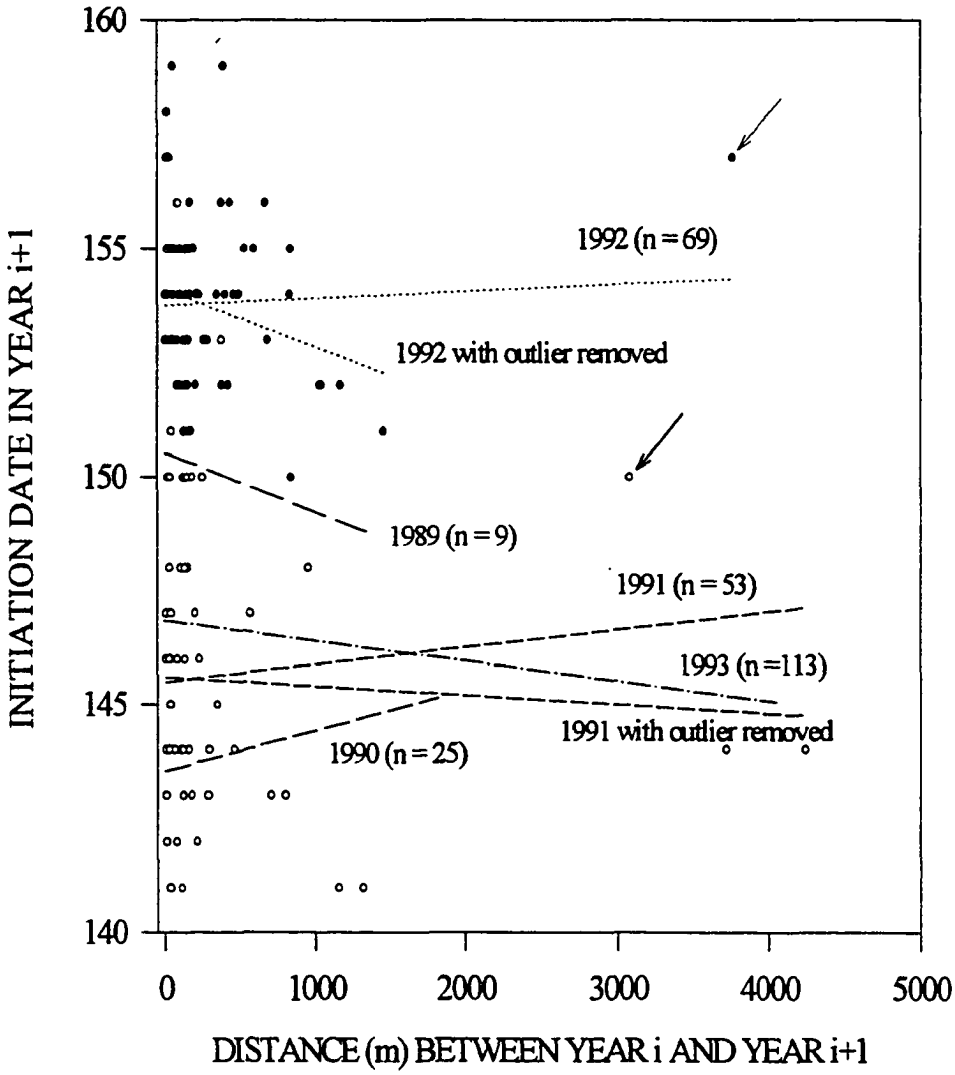

FIGURE 6. Relationship between dispersal distance (year *t* to year *t*+1) and nest initiation date for Black Brant nesting at Tutakoke River, Alaska, 1989-1993. Data points are shown for 1991 (open circle) and 1992 (closed circle). Influential points are identified with an arrow.

EFFECTS OF SPRING ENVIRONMENT ON NESTING PHENOLOGY, NEST-SITE SELECTION, AND CLUTCH SIZE OF BLACK BRANT[1]

Abstract: From 1986-1993, we studied effects of timing of spring snowmelt on nesting phenology, nest-site selection, and clutch size of Black Brant (*Branta bernicla nigricans*) breeding at the Tutakoke River colony, Alaska. In late springs, brant delayed nest initiation; however, time between peak arrival at Tutakoke and nest initiation (7 to 11 days) was similar in early and late springs. Brant nesting at Tutakoke may be better able to time migration with snowmelt conditions on breeding areas than brant nesting in the Arctic because of proximity of spring staging areas to breeding areas. Nest initiation was more synchronized in late springs than early springs. In late springs, height of nests relative to spring meltwater levels was lower indicating that the interval between snowmelt and nest initiation was shorter. Reduced availability of nest sites and increased nesting synchrony in late years may result in greater competition for available nest sites and reduced site fidelity. Clutch size was greater in late springs than in early springs. This

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increase in clutch size may result from greater accumulation of endogenous reserves on spring staging areas in late springs, or more simply, from demographic changes in the population.

Key words: Alaska, Black Brant, Branta bernicla nigricans, *clutch size, nest initiation, nest site selection.*

INTRODUCTION

Numerous studies have investigated effects of spring environment on nesting phenology and reproductive performance of northern nesting geese and some eiders (Barry 1962, Barry 1967, Bruggink et al. 1994, Cooke et al. 1995, Ely and Raveling 1984, Laurila and Hario 1988, MacInnes et al. 1974, MacInnes and Dunn 1988, Mickelson 1975, Petersen 1992, Prop and de Vries 1993, Raveling and Lumsden 1977, Raveling 1978). The response of geese to spring environmental conditions is variable, however, and researchers have documented latitudinal and species-specific variation in response of geese to spring environments (Raveling 1978). Several studies showed that delays in nesting resulted in reduced clutch size (Mickelson 1975, Raveling 1978, Ely and Raveling 1984, MacInnes and Dunn 1988) or in extreme cases, greatly reduced breeding probability (Cooch 1961, Barry 1962, MacInnes and Dunn 1988), whereas other studies have observed little or no effect of spring phenology on reproductive performance (Petersen 1992, Bruggink et al. 1994). Reproductive performance relative to environmental conditions is likely influenced

by interspecific variation in reproductive strategies or intraspecific variation in reproductive strategies across latitudes.

Raveling (1978) suggested that geese nesting in Arctic and sub-Arctic regions express among-species variation in nesting phenology relative to spring environment because of variation in timing of rapid follicle development. He proposed that geese nesting in the high Arctic and species with long periods of incubation and gosling development commenced rapid follicle development during spring migration so they could initiate nesting soon after arrival on the breeding grounds (Raveling 1978). This strategy potentially results in greatly reduced reproductive performance in late springs if nest sites are unavailable until after completion of follicle development. Females that experience these conditions may reabsorb developing follicles (Raveling 1978), abandon nesting (Cooch 1961), or lay their eggs in nests of other geese (Syroechkovsky 1979, Cooke et al. 1995). In contrast, Raveling (1978) suggested goose species nesting at lower latitudes or those requiring less time for incubation and gosling growth exhibited a more conservative reproductive strategy, using departure from spring staging areas or arrival on the breeding grounds as the stimulus for rapid follicle development. This strategy provides a more flexible response to weather conditions in spring. Recent studies (Ely and Raveling 1984, MacInnes and Dunn 1988) have generally supported Raveling's (1978) premise (but see Bruggink et al. 1994); however, his hypothesis remains largely untested (but see Hamann et al. 1986).

Our goals were to test Raveling's (1978) hypothesis for Black Brant, *Branta*

bernicla nigricans, (hereafter brant) breeding on the Yukon-Kuskokwim Delta (YKD), Alaska. The YKD is sub-Arctic (ca. 61°N) breeding area, and brant require a shorter time for gosling development (ca. 40 days, Bellrose 1980) relative to other geese. We therefore predicted that brant would exhibit a conservative reproductive strategy, and time between arrival on the breeding areas and nest initiation would approximate time required for rapid follicle development. Furthermore, we predicted that brant would not experience follicular atresia in late springs. We could not directly assess effect of spring environment on follicle development, but we instead measured clutch size of brant. We further explored latitudinal variation in nesting phenology of brant by comparing our findings with previous studies of brant nesting in the Arctic (Southampton Island and Anderson River Delta, N.W.T.) (Barry 1962, Barry 1967). Finally, we investigated effects of spring environment on nest-site selection by examining the relationship between snowmelt and characteristics of nest sites used by brant.

STUDY AREA

The Tutakoke River brant colony (61°15' N 165°35'W) is located on the Bering Sea coast of the Yukon-Kuskokwim River Delta (YKD), Alaska (Fig. 1). Most brant at Tutakoke nested in sedge meadows within 1 km of the coast. Spring breakup at Tutakoke River (mid-May to early June) was characterized by water from melting snow collecting in meltwater lakes, which were contained by higher-elevation levees on the coast and along tidal sloughs. Water in these lakes drained when ice dams in coastal sloughs melted. Typically, coastal levees were the first areas free of snow and meltwater. Drainage of

meltwater lakes generally preceded from the northern to the southern portion of the colony. Because of intra-colony differences in timing of snowmelt, we stratified the colony into 4 areas (strata A-D, Fig. 1) that are described in more detail in Lindberg et al. (1995).

METHODS

SNOWMELT AND SPRING MIGRATION

We used the date the colony was 100% snow-free as an index of timing of spring. Because data on time of 100% snow melt were not available for Tutakoke River in 1986, we used snow melt data from a research camp (Old Chevak) located approximately 20 km to the northeast of Tutakoke for that year. Range of dates for 100% snow melt exhibited a clear dichotomy for both Tutakoke and Old Chevak sites. We classified 1986, 1988, 1990, 1991 and 1993 as early springs, which were 100% snow free between 17-21 May at Tutakoke and between 6-13 May at Old Chevak. The remaining 3 years (1987, 1989, 1992) were classified as late, because 100% snow melt occurred between 28 May - 2 June at Tutakoke and 18-22 May at Old Chevak.

We counted brant during spring to estimate peak arrival date at Tutakoke. Estimates of peak arrival were based on observations conducted from 5 m high towers for 2 hr each day. Because of differences in protocols for data collection protocol incomplete tower counts, peak arrival was not estimated in 1987 or 1991 .

NEST INITIATION AND CLUTCH SIZE

From 1987 to 1993, we located brant nests using 2 techniques. First, nest were located by

searching 50 m radius plots (n = 34 to 49) located in a stratified, random design throughout the breeding colony. We began searching for nests on plots as soon as the first eggs were laid in spring (mid-May to early June), and we continued searches through the end of egg laying (early to mid-June). Each plot was searched every 4th day. While traveling between plots, we also located nests of brant previously marked with tarsal tags (Sedinger et al. 1995). During late incubation, we intensified our search for nests of marked brant by systematically searching the colony every 1-2 days. For all nests, we recorded number of eggs and nesting stratum (see strata designations Fig. 1), and we labeled eggs for future identification. We calculated initiation dates for nests discovered during laying by back dating from the date the nest was located and assuming that 1 egg was laid each day. For nests not discovered during laying but with a known hatching date, we back dated from the hatching date to calculate initiation date, assuming 24 days of incubation and that incubation began when the second egg was laid (Flint et al. 1994). Clutch size was defined as the maximum number of eggs observed in the nest. To minimize bias in estimates of clutch size created by partial predation before we located a nest, we only used nests discovered during laying to determine clutch size. We excluded nests with >7 eggs (n = 9) because these clutches may have resulted from parasitic egg-laying.

We tested for strata and year variation in nest initiation dates using ANOVA (PROC GLM, SAS Inst. Inc. 1990). We followed this ANOVA with a contrast (Neter et al. 1985:570-572) to examine a planned comparison of initiation dates in early and late

springs. We tested the hypothesis that nesting was more synchronized in late springs than early springs by comparing the variance of initiation dates in late and early springs (Snedecor and Cochran 1980:98-99). We used tests of skewness (Snedecor and Cochran 1980:98-99) to compare distributions of nest initiation dates in early and late springs.

We tested for differences in clutch size among years and strata with ANCOVA (PROC GLM, SAS Inst. Inc. 1990). We included initiation date as a covariate in the ANCOVA model because clutch size declines with initiation date (Flint and Sedinger 1992). The covariate, initiation date, was expressed as deviation in days from the modal initiation date for each year. We examined differences in clutch size in late and early springs with a contrast (Neter et al. 1985:570-572). We tested the hypothesis that the distribution of clutch sizes was independent of spring phenology (i.e., early vs. late) with χ^2 test of independence (PROC FREQ, SAS Inst. Inc. 1990).

NEST HEIGHT

From 1986-88 and in 1992 we determined height of nests relative to spring meltwater by marking and dating water levels on gauges located in 2 ponds (plots 22 and 41) in stratum C (Figs. 1 & 2). Water levels were marked approximately every 3 days (range 2 - 5 days) before and during nest initiation. We used linear interpolation to estimate levels of meltwater between dates when water level was measured. After completion of incubation, we used line-levels and transits to determine height of nests relative to the pond bottom (H_p) and relative to meltwater depth on the date the nest was initiated (H_w) (Fig. 2). A negative value for H_w indicated that the nest was flooded when the first egg was laid and a

positive value indicated the nest was above meltwater depth on the initiation date. H_p and H_w were recorded for a random sample of nests within approximately a 100 m radius of the pond gauge.

We used ANCOVA (PROC GLM, SAS Inst. Inc. 1990) to examine the relationship between H_p and initiation date among years and plots. Initiation date was expressed as deviation in days from the modal initiation date for each year. Because H_p was measured relative to the pond bottom and height of pond bottoms varied across years and plots, these heights were not comparable across years or plots. Therefore, we only tested for differences in the slope of the relationship between H_p and initiation date between plots, among years, and among years within plots.

We used ANCOVA (PROC GLM, SAS Inst. Inc. 1990) to examine year and plot variation in H_w. Initiation date was included as a covariate. Unlike H_p, H_w was comparable across years and plots. We used linear contrasts (Neter et al. 1985: 570-572) to compare H_w in late and early springs.

RESULTS

The difference in the average date of 100% snow melt for late and early springs was 10 days (Fig. 3). Time between peak arrival and peak nest initiation ranged from 7 to 11 days averaging 10 days in late years (1989 and 1993) and 9 days in early years (1988, 1990, 1993).

NEST INITIATION AND CLUTCH SIZE

We obtained nest initiation dates for 3,556 nests between 1987-93. Initiation date varied

among years ($F = 680.81$, df = 6, 3,528, $P < 0.001$) and strata ($F = 4.98$, df = 3, 3,528, $P = 0.002$) and pattern of initiation dates varied among strata over years (year*strata interaction, $F = 3.31$, df = 18, 3,528, $P < 0.001$) (Fig. 3). Mean initiation date in late springs (2 June, SE = 0.08, $n = 1,424$) was 7 days later ($F = 533.96$, df = 1, 3,528, $P < 0.001$) than mean initiation date (26 May, SE = 0.07, $n = 2,132$) in early springs and peak (modal) initiation dates differed by 6 days (late spring = 1 June, early spring = 26 May). Variance of initiation date in early years (11.4 days) was greater ($F = 1.15$, df = 2,132,1,424, $P = 0.003$) than variance in late years (9.9 days) indicating that nesting was more synchronized in late years (Fig. 4). Distribution of nest initiation dates was positively skewed ($P < 0.01$) in both early and late years (Fig. 4).

From 1987-1993 we measured clutch size for 1,751 nests (Table 1). We observed no significant variation in clutch size among strata ($F = 0.75$, df = 3,1,624, $P = 0.52$) and data were therefore pooled across strata. Clutch size varied among years ($F = 5.07$, df = 6,1,737, $P < 0.001$). We observed a negative relationship between clutch size with initiation date ($F = 181.64$, df = 1,1,737, $P < 0.001$); however, this relationship was not constant across years ($F = 2.77$, df = 6,1,737, $P = 0.01$) (Fig. 5). Mean clutch size (least square estimates) in late springs ($\bar{X} = 4.40$, SE = 0.03, $n = 804$) was greater ($F = 25.64$, df = 1,1,737, $P < 0.001$) than mean clutch size in early springs ($\bar{X} = 4.23$, SE = 0.03, $n = 947$). Distribution of clutch sizes was not independent of spring phenology ($\chi^2 = 36.3$, df = 5, $P < 0.001$), which was largely explained by a change in the proportion of 5-egg clutches (Fig. 6). Five-egg clutches accounted for 45% ($n = 804$) of clutches in late

springs and only 34% (n = 947) in early springs.

NEST HEIGHT AND DENSITY

No annual variation occurred in the relationship between H_p and initiation date across ($\underline{F}$ = 2.52, df = 3,193, P = 0.06) or within plots (F = 2.34, df = 3,193, $\underline{P}$ = 0.07) (Fig. 7). Brant nesting later used lower-elevation nest sites (F = 10.3, df = 1,199, P = 0.002) and the decline in H_p with later nest initiation was steeper (F = 9.05, df = 1,199, P = 0.003) on plot 22 (β = -1.06) than plot 41 (β = -0.03) (Fig. 7).

H_w varied among years (F = 5.29, df = 3,193, P = 0.002), between early and late springs (F = 8.49, df = 1,193, P = 0.004), and between plots (F = 41.91, df = 1,193, P < 0.001) (Fig. 8). In late springs, mean (least squares estimate) H_w was negative (i.e., below meltwater level) when nests were initiated (H_w = -1.31, SE = 0.67, n = 48, 1987; H_w = -2.00, SE = 1.08, n = 17, 1992), whereas in early years mean H_w was positive (H_w = 0.25, $\hat{SE}$ = 0.51, n = 86, 1986; H_w = 0.70, SE = 0.63, $\underline{n}$ = 55, 1988). Nests on plot 22 (H_w = 1.67, $\hat{SE}$ = 0.41, $\underline{n}$ = 155) were higher relative to meltwater levels than those on plot 41 (H_w = -2.85, $\hat{SE}$ = 0.64, $\underline{n}$ = 51). H_w increased (F = 36.40, df = 1,193, P < 0.001) with later nest initiation indicating that meltwater levels receded faster than declines in elevation of nests used by brant. Increase in H_w with later nest initiation did not vary among years (F = 1.30, df = 3,193, P = 0.28) or between plots (F = 1.39, df = 1,193, P = 0.24).

DISCUSSION

NESTING PHENOLOGY

The interval between peak arrival and peak nest initiation we observed (7 to 11 days) (Fig.

3) approximated the time required for rapid follicle development in geese (12 days, Alisauskas and Ankney 1992). Based on Barry's (1962, 1967) studies of Atlantic (*B. b. hrota*) and Black Brant in the Arctic, Raveling (1978) hypothesized that brant initiate rapid follicle development upon departure from the last spring staging area or upon arrival on the nesting area. Our results are consistent with his (Raveling 1978) prediction. In addition, the interval between arrival and nest initiation was similar in early and late springs; even though nest sites were available several days prior to onset of nesting in early springs. Therefore, brant were unable to take full advantage of early springs, which may reflect a cost associated with their strategy of follicle development.

We did not observe intervals between peak arrival and initiation >11 days as Barry (1962) reported for brant in the Arctic. Brant breeding at Tutakoke maintained a stable arrival to initiation interval by nesting earlier relative to spring phenology in late springs (see also MacInnes and Dunn 1988) (Fig. 8). Furthermore, complete reproductive failure, which Barry (1962) reported for brant nesting in the Arctic, has not been observed for brant breeding on the YKD (Raveling 1978, this study). This difference may be related to proximity of spring staging areas to nesting areas and, therefore, the ability of brant to predict snowmelt conditions on breeding grounds (cf. Petersen 1992). Izembek Lagoon, Alaska, is the principal staging area for brant (Ward and Stehn 1989) during spring migration; however, little is known about migration corridors following departure from that area (Cade 1955). Barry (1967) suggested that brant required from 3 to 6 days for migration from Izembek to the breeding grounds at Anderson River, N.W.T. Despite 21

days variation in spring thaw (ice out of Anderson River), Barry (1967) reported only a 5-day range of first arrival dates from 1959-63. In contrast, brant breeding at Tutakoke likely use Chagvan and Nanvak bays, Alaska, as final staging areas following departure from Izembek (D.H. Ward, unpubl. data), a distance of 350 km from Tutakoke River. We observed a 12-day range in peak arrival dates at Tutakoke, and arrival dates paralleled date of 100% snowmelt.

CLUTCH SIZE

Clutch size of brant nesting at Tutakoke increased in late springs. In contrast, previous studies of northern nesting geese have observed reduced clutches in late springs (Barry 1962, Raveling 1978, Dau and Mickelson 1975, Ely and Raveling 1984, MacInnes and Dunn 1988) or no relationship between time of spring thaw and clutch size (Bruggink et al. 1994, Petersen 1992). In other studies, declines in clutch size in late springs were correlated with increased delays between arrival and nest initiation (Barry 1962, Raveling 1978, Dau and Mickelson 1979, Ely and Raveling 1984, MacInnes and Dunn 1988), which presumably resulted in use of reproductive reserves for maintenance and atresia of developing follicles (Raveling 1978, MacInnes and Dunn 1988). Others (Budeau et al. 1991, Gauthier and Tardif 1991, Bruggink et al. 1994, Sjöberg 1994) have argued that feeding upon arrival at breeding areas may allow geese to conserve or augment endogenous reserves acquired during spring migration.

We do not believe that increased food intake on the breeding grounds during the prenesting period in late springs augmented endogenous reserves of brant at Tutakoke.

Brant were not present on the breeding areas during the prenesting period for longer periods in late springs than early springs. In addition, brant nested earlier relative to spring thaw in late springs and food resources were therefore probably less available during prenesting in late springs, compared with early springs (Prop and de Vries 1993). Nonetheless, if date of arrival on staging areas is consistent among years, brant may experience increased foraging time on spring staging areas in late springs. Female brant staging at Izembek Lagoon during the fall increase body weight by approximately 7.8 g/day (Dau 1992). Ebbinge and Spaans (1995) suggested that reproductive performance of Brent Geese (*B. b. bernicla*) is postively correlated with reserves accumulated on spring staging areas. Therefore, in late springs, females may arrive on breeding grounds with more reserves than in early springs because of increased foraging time on spring staging areas.

Alternatively, increased clutches in late springs may reflect reduced breeding propensity by younger brant. Clutches of 2-year-old brant are significantly smaller than clutches of brant >2 years old (Flint and Sedinger 1992). If proportionally fewer 2-year-old brant nest in late springs, then the increase in clutch size we observed may reflect a change in the age structure of brant nesting at Tutakoke.

We attempted to reduce sources of bias in estimates of clutch size by limiting our sample to nests discovered during laying. Cooke et al. (1995) noted 2 additional sources of bias in clutch-size estimates; nest parasitism and nest failure during pre-incubation. Parasitic egg laying has been observed in brant, and an increase in the rate of nest

parasitism during late spring could explain the increased clutch size we observed. In late springs, however, the increase in clutch size was largely the result of a proportional increase in 5-egg clutches, which are commonly observed in brant (Flint and Sedinger 1992), rather than an increase in clutches >6 (Fig. 6). Nest failure in pre-incubation may negatively bias estimnates of clutch size because females lay smaller clutches in subsequent nesting attempts (i.e., continuation clutches, Cooke et al. 1995). Although we observed continuation clutches in brant (Lindberg et al. unpubl. data), we have no data suggesting a higher rate of continuation nesting in early springs. Nest abandonment we detected during laying was 0.8% (n = 3,530) in early springs and 0.9% (n = 2,314) in late springs.

NESTING SYNCHRONY AND SITE SELECTION

Our finding of more synchronized nesting in late springs than in early springs is consistent with previous studies of northern-nesting geese (Ryder 1972, Mickelson 1975, Raveling 1978, Ely and Raveling 1984, Bruggink et al. 1994). Increased nesting synchrony and reduced availability of nest sites caused by meltwater flooding in late springs may have implications for behavior of brant during nest initiation. Barry (1962) suggested aggression among nesting brant was more intense in late springs than in early ones. Although female brant generally return to previously-used nest sites (Lindberg et al. 1995), site fidelity may be reduced in late springs if previously used nest sites are flooded when females initiate nesting (Abraham 1980).

Distribution of initiation dates for brant at Tutakoke were positively skewed in both early and late springs. We suggest that brant maintain earliest possible nesting in late

springs by dispersing to available nest sites when traditional sites are unavailable at the time of nesting (Lindberg and Sedinger unpubl. data). Findlay and Cooke (1982) observed a positive skew in the distribution of initiation dates for Lesser Snow Geese (*A. c. caerulescens*) in early springs and a negative skew in late springs. They (Findlay and Cooke 1982) suggested that changes in these distributions were the result of differences in the availability of nest sites. Fewer nest sites were available during early initiation in late springs. In early springs, nest-site availability was not a limiting factor, and the positive skew reflected selection for early nesting (Cooke et al. 1995). Selective pressures for early nesting may be more prevalent in late years. Brant with earlier hatching dates had greater growth, survival, and fecundity than brant with late hatch dates (Sedinger and Flint 1991, Sedinger et al. 1995) because availability of high quality foods declines during the season (Sedinger and Raveling 1986). Cooch et al. (1991) suggested that declines in growth rates of goslings may be steeper in late springs than early springs. The inability of brant to immediately exploit available nest sites in early springs and the conservative strategy of timing of follicle development exhibited by these geese suggests that higher costs are associated with nesting later in late springs than early springs.

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Table 1. Least-squares estimates of mean clutch size for brant nesting at the Tutakoke River colony, Alaska, 1987-1993.

Year	*n*	Mean	SE
1987	285	4.37	0.05
1988	276	4.24	0.05
1989	285	4.43	0.05
1990	219	4.20	0.06
1991	223	4.25	0.06
1992	234	4.41	0.06
1993	229	4.13	0.06

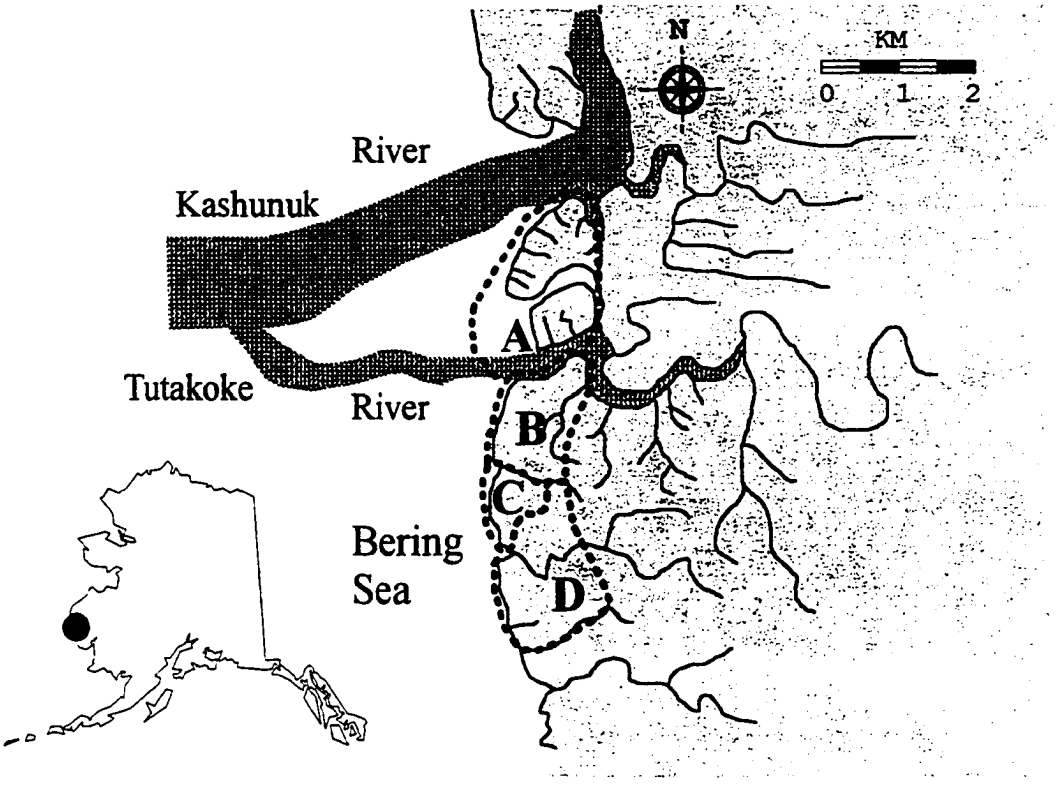

FIGURE 1. Location of the Tutakoke River Black Brant colony on the coast of the Yukon-Kuskokwim River Delta, Alaska. Strata boundaries are shown with dashed lines and each stratum is designated with a capital letter (A-D).

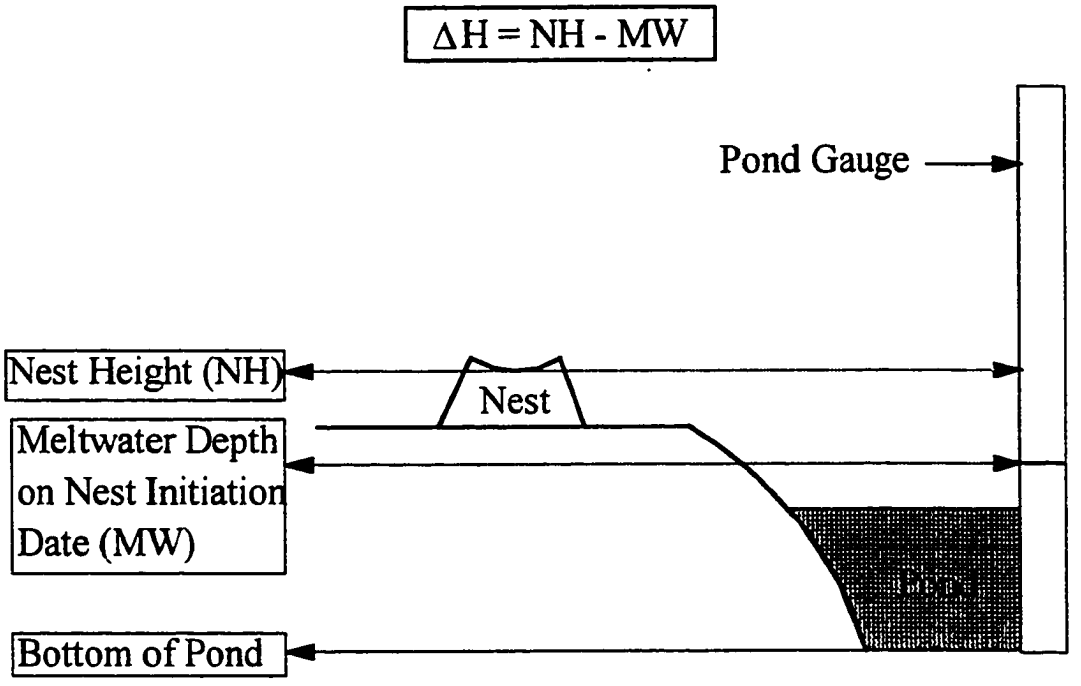

FIGURE 2. Diagram of technique used to determine height of nests relative to meltwater depth on the day the nest was initiated. NH and MW were recorded from either the bottom of the pond or the pond water level on the day the measurements were taken and were measured with line levels or transits.

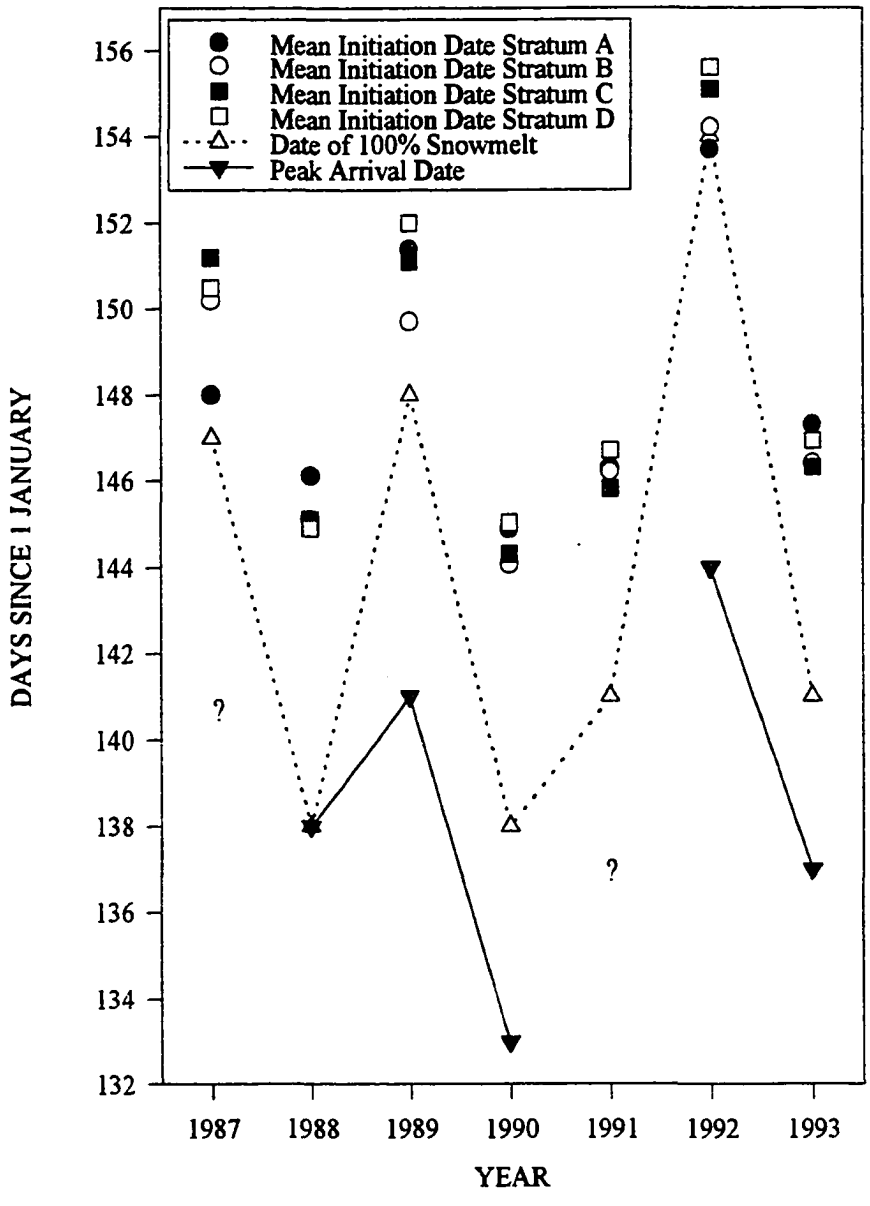

FIGURE 3. Mean initiation dates by strata for brant nesting at the Tutakoke River colony, Alaska, 1987-1993. Date the colony was 100% snow free is shown by a dashed line and peak arrival date is shown by a solid line. Date of peak arrival was not available in 1987 or 1991.

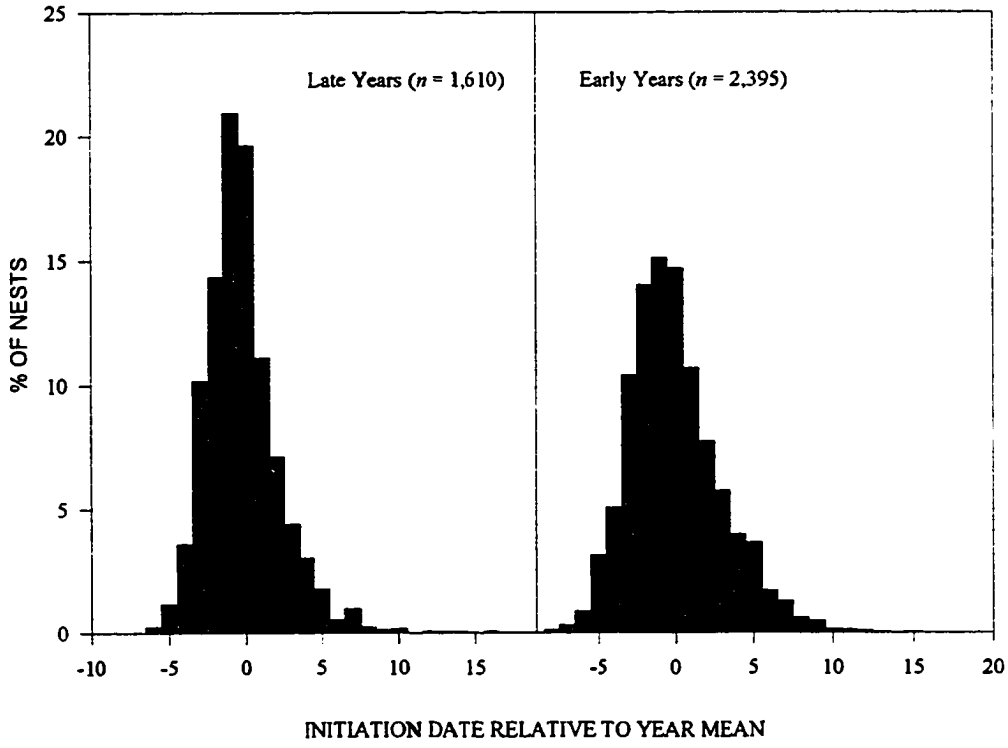

FIGURE 4. Distribution of nest initiation dates in early (1987, 1989, 1992) and late springs (1988, 1990, 1991, 1993) for brant at the Tutakoke River colony, Alaska.

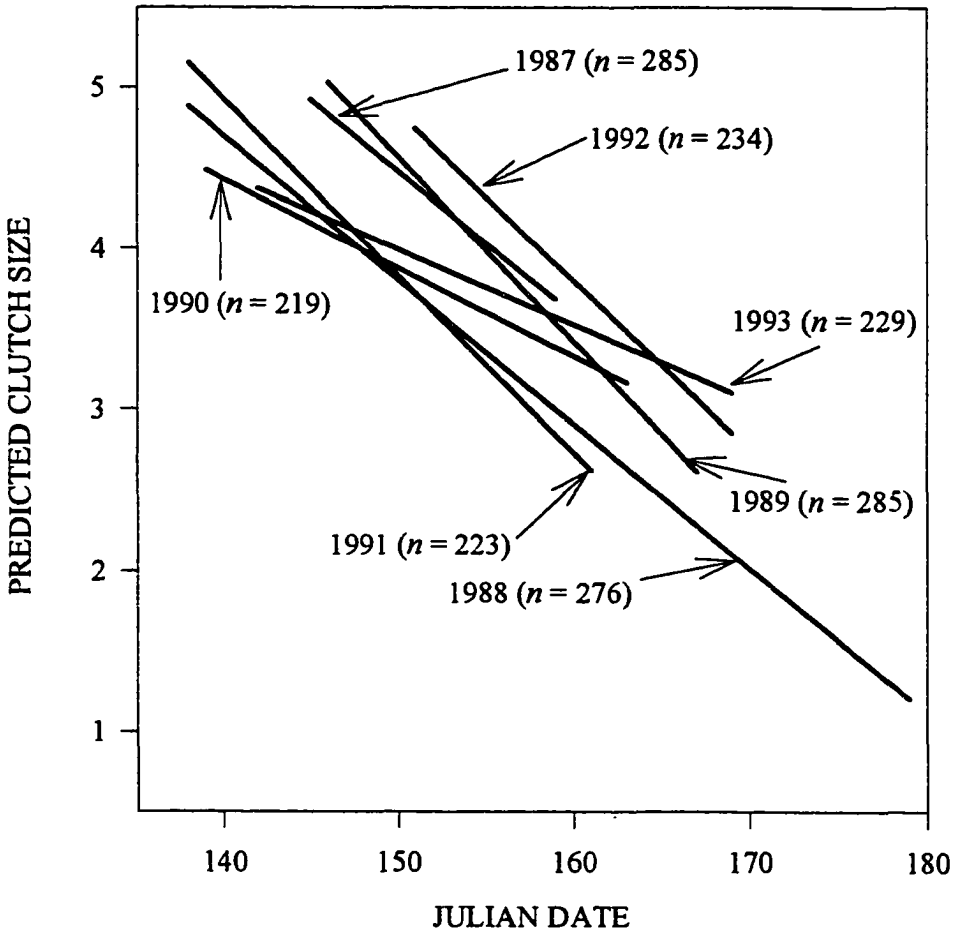

FIGURE 5. Relationship between clutch size and initiation date for Black Brant nesting at the Tutakoke River, Alaska, 1987-1993.

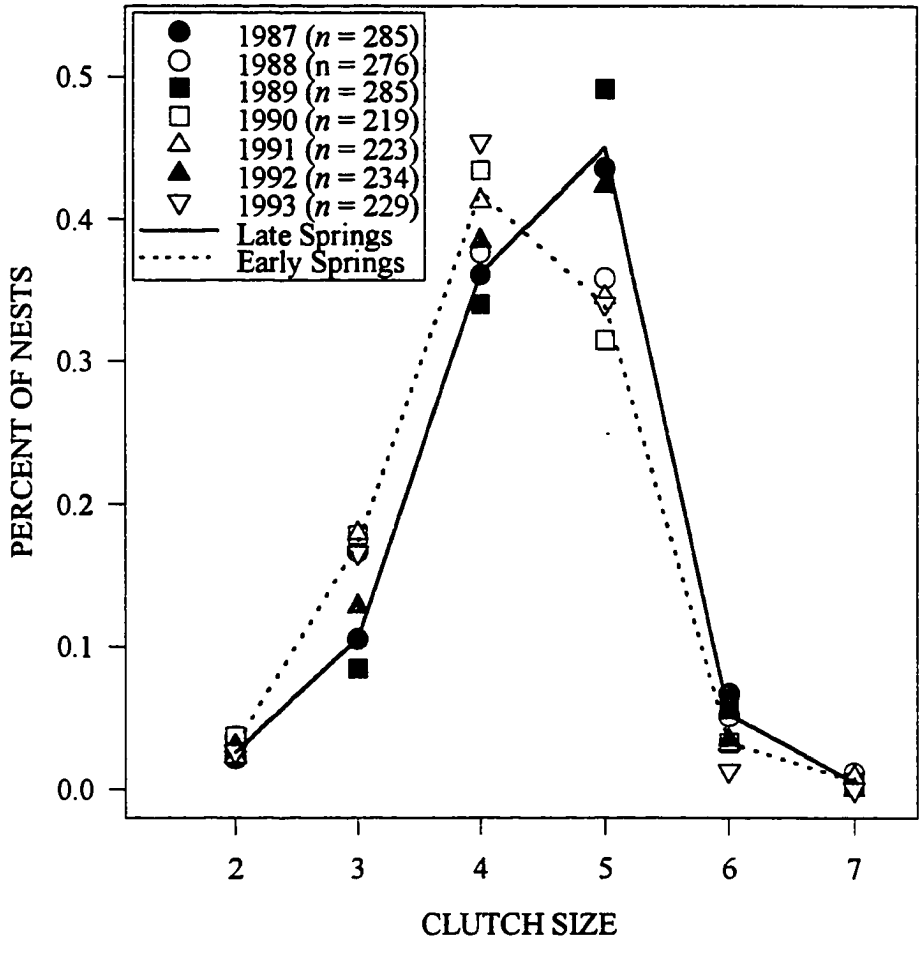

FIGURE 6. Distribution of clutch sizes for Black Brant nesting at the Tutakoke River, Alaska, 1987-1993. Mean percent of clutch sizes is shown with a solid line for late springs (1987, 1989, 1992; closed symbols) and a dashed line for early springs (1988, 1990, 1991, 1993; open symbols).

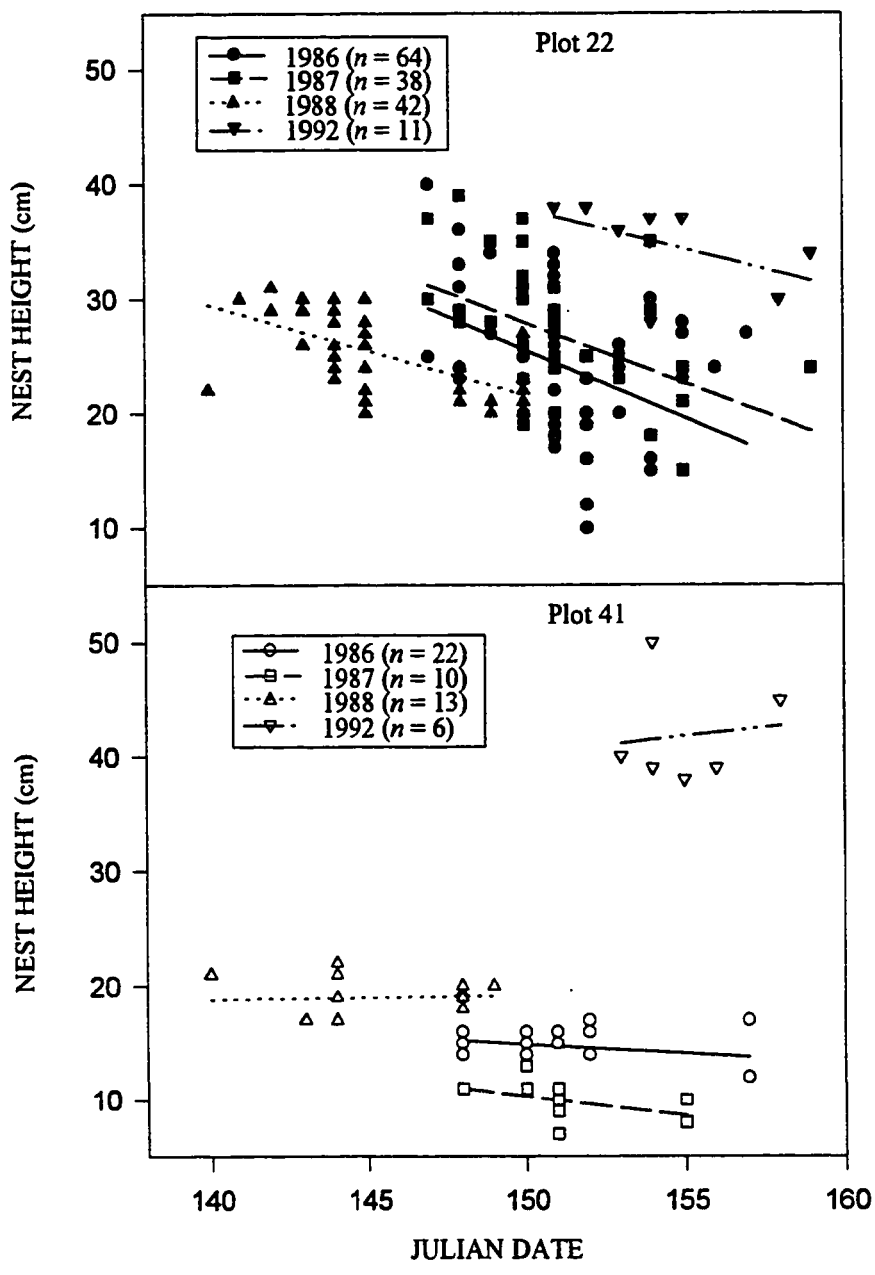

FIGURE 7. Relationship between nest height relative to pond bottom (1986, 1987, 1992) or water level (1988), and initiation date for brant nests on 50 m radius plots (plot 22 and 41) of the Tutakoke River colony, Alaska.

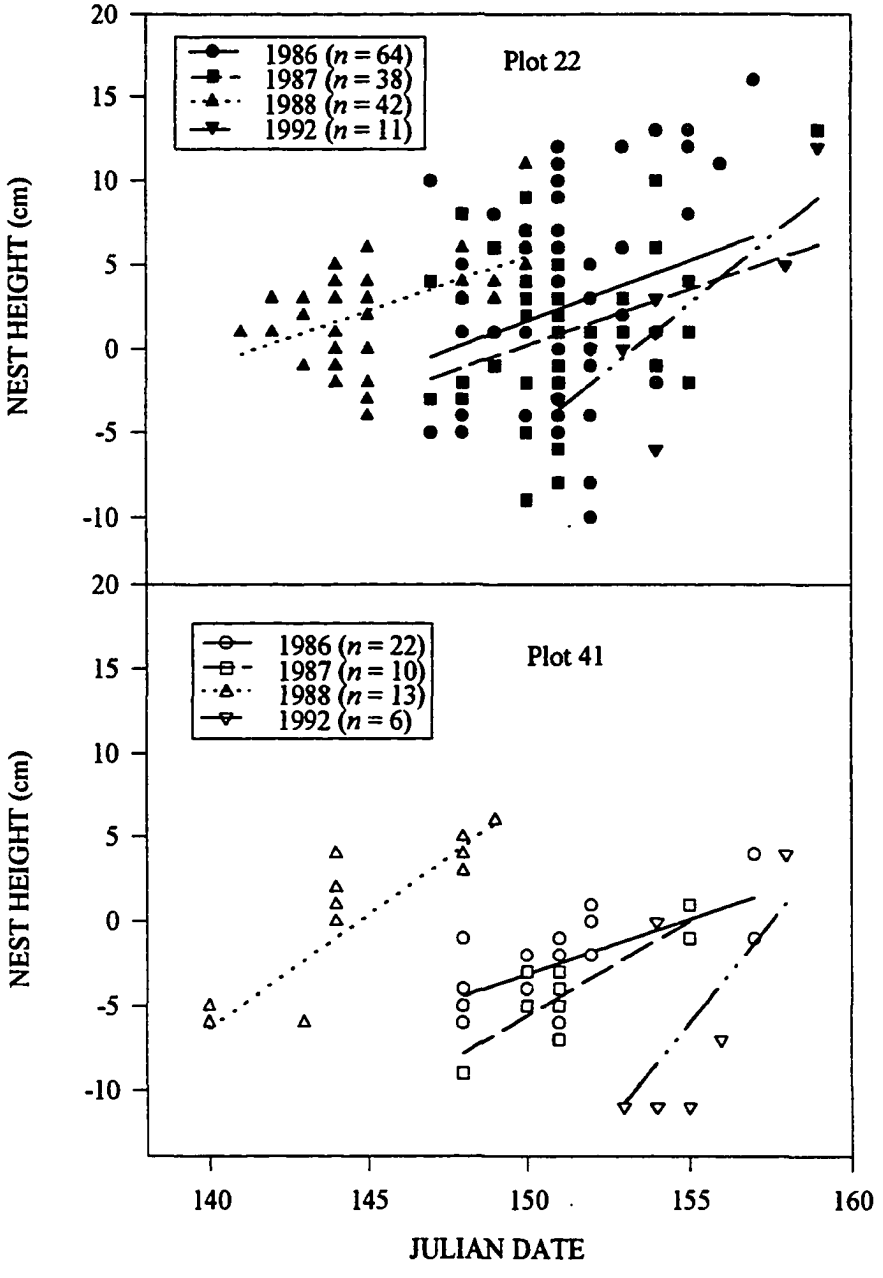

FIGURE 8. Relationship between nest heights relative to meltwater levels and initiation date for brant nests on 50 m radius plots (plot 22 and 41) at the Tutakoke River colony, Alaska, 1986-88, and 1992.

POPULATION STRUCTURE AND NATAL AND BREEDING MOVEMENTS IN A BLACK BRANT METAPOPULATION[1]

Abstract: We estimated natal and breeding philopatry and dispersal probabilities for a metapopulation of Black Brant (*Branta bernicla nigricans*) based on observations of marked brant at 6 breeding colonies in Alaska, 1986-1994. Both adult females and males exhibited high (>0.90) probability of breeding philopatry. Probability of natal philopatry was significantly higher for females than males. Natal dispersal of males was recorded between every pair of colonies, whereas natal dispersal of females was observed between only half of colony pairs. We suggest that female-biased philopatry was the result of timing of pair formation and characteristics of the mating system of brant, rather than factors related to inbreeding avoidance or optimal discrepancy. An increase with age in probability of natal philopatry of females resulted from an increase in breeding propensity. For females, probability of natal philopatry declined with year of banding, whereas probability of permanent emigration increased. Trends in natal philopatry of females corresponded to a period of increasing population density and local population density

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may therefore influence probability of nonbreeding and gene flow among colonies.

Key words: Alaska; Black Brant; Branta bernicla nigricans; *density dependence; dispersal; emigration, gene flow, immigration, multi-state models; philopatry.*

INTRODUCTION

Movement of individuals among populations and fidelity of individuals to natal breeding areas affects not only the distribution and size of populations, but also has important implications for their genetic structure (Rockwell and Barrowclough 1987). Despite the potential importance of fidelity and dispersal for population dynamics and structure few, studies have examined dispersal because of logistical constraints associated with these studies.

In birds, direct measurements of dispersal and fidelity began only recently, as marking and reobservation techniques became more widely used (Greenwood and Harvey 1982, Rockwell and Barrowclough 1987, Anderson et al. 1992). Although dispersal patterns have been documented in some species (Greenwood and Harvey 1982, Rockwell and Barrowclough 1987, Anderson et al. 1992), estimation of movement probabilities is still frequently based on inappropriate statistical models (Johnson et al. 1992). Most studies are based on return of individuals to a single study site. For example, return rate, which is the product of survival, detection, and homing probability, is the most common parameter estimated in studies of birds (Anderson et al. 1992, Johnson et al. 1992). Interpretation of return rates is hampered by variation in survival and detection

probabilities among species, sexes, or populations. A renewed interest in estimating animal movements has resulted in development of new statistical approaches and software (Brownie et al. 1993). For example, recent studies employing these methodologies documented high probabilities of site fidelity in in winter for Canada Geese, *Branta canadensis*, (Hestbeck et al. 1991) and movement rates in a metapopulation of Roseate Terns, *Sterna dougallii*, (Spendelow et al. 1995). Nonetheless, there is a paucity of data on movement rates for many groups of birds (Rockwell and Barrowclough 1987).

Among birds, waterfowl exhibit an almost unique pattern of philopatry in which females generally return to natal breeding areas and males disperse (Greenwood and Harvey 1982, Rohwer and Anderson 1988, Anderson et al. 1992). Greenwood (1980) proposed that female-biased dispersal in waterfowl was largely the result of a mate-defense mating system rather than resource-defense mating system prevalent in other birds. Studies of species exhibiting sex reversals and resource defense by females (Oring and Lanke 1982, Oring and Lank 1984, Reynolds and Cooke 1988) have supported Greenwood's (1980) hypothesis. Rohwer and Anderson (1988) generally agreed with Greenwood (1980), but expanded the hypthesis to include timing of pair formation as an important determinant of female-biased philopatry. Detection of female-biased philopatry was largely based on observations of lower return rates for male than for female waterfowl to a single study site (Anderson et al. 1992). As a result, most of these studies are plagued by a confounding of mortality, emigration, and detection probability. Moreover, estimates of dispersal among populations and estimates of natal philopatry are generally

lacking (Anderson et al. 1992).

We studied emigration and immigration in a metapopulation of Black Brant (*Branta bernicla nigricans*) (hereafter brant) by observing individually marked brant at 6 breeding colonies, which included approximately 80% of the breeding population (Sedinger et al. 1993). Our goals were to obtain estimates of breeding and natal philopatry unconfounded with emigration and detection probabilities, to examine age-related variation in patterns of natal philopatry, to investigate competing hypotheses (Greenwood 1980, Shields 1983, Rohwer and Anderson 1988) used to explain female-biased philopatry in waterfowl, and to examine effects of density on philopatry. Because our sampling included most of the breeding populations, we were able to directly test sex-biased differences in probability of emigration rather than simply comparing return of males and females to a single study site. We tested for evidence of positive or negative assortative mating in brant by comparing our estimates of male philopatry to that expected under a hypothesis of random mating.

METHODS

Banding and observations of marked brant

Beginning in 1985, brant were captured in July and August during the adult remigial molt. Both goslings and adults were marked with U.S. Fish and Wildlife Service legbands and 2.5 cm high, plastic tarsal tags (Sedinger et al. 1995). Tarsal tags were engraved with an unique, 3 character alphanumeric code. These tags could be read with the aid of 60 X spotting scopes at a distance of up to 300 m.

Brant were banded at 4 breeding colonies in Alaska (Fig. 1): Tutakoke River (1986-1994), Colville River (1990-1992), Prudhoe Bay (1991-1994), and Kokechik Bay (1990-1991, 1993-1994). Additional banding was conducted at areas used predominantly by molting brant, Wrangell Island, Russia (1989-1992), Teshekpuk Lake, Alaska (1990-92), and western Arctic, N.W.T., Canada (1990-1994) (Fig.1). Recaptures of previously banded brant were recorded during banding operations at each location. During summer (May-July) 1986-1994, we read tarsal tags of marked brant at breeding colonies with the aid of binoculars or spotting scopes. Observations of marked brant were obtained during nesting or following hatching, when goslings and adults occupied brood rearing sites near breeding colonies. Marked brant were observed at Tutakoke River (1986-1994), Kokechik Bay (1990-1991, 1993-1994), Colville River (1990-1994), Baird Inlet Island, Alaska (1990-1992), Kigigak Island, Alaska (1990-1993), and Prudhoe Bay (1991-1994) (Fig. 1).

Definitions and approach to analyses

Terminology used in the study of animal movements has changed with time and species under study (Rockwell and Barrowclough 1987). We largely adopted the terminology proposed by Greenwood (1980) and Greenwood and Harvey (1982; see also Rockwell and Barrowclough 1987, Anderson et al. 1992). Natal philopatry refers to return of brant to their colony of birth in subsequent breeding attempts. Return and breeding at the colony of the last breeding attempt, when natal colony is unknown, is called breeding philopatry. Natal and breeding dispersal are defined as movement from

place of birth (natal) or location of subsequent breeding (breeding) to site of next breeding attempt. Use of these terms implies that the breeding status was recorded for each individual we included in our analysis. We discuss implications of departures from this assumption, particularly for estimates of dispersal. We use permanent emigration to describe individuals that fail to return to natal sites. Permanent emigrants, therefore, include both individuals breeding at new sites and individuals that are permanent nonbreeders. We use temporary emigration to describe individuals that are temporarily absent from their previous breeding site or site of birth , but are philopatric to the natal or breeding colony at some point during the study. We use movement probabilities to collectively refer to natal or breeding philopatry and dispersal.

Our original intent for these analyses was estimating movement probabilities (1990-1994) among all breeding colonies sampled during our study with multistate modeling (Brownie et al. 1993). A required component of this statistical approach is that all possible movements between pairs of colonies are recorded during each year of the study. We were unable to meet these criteria because landowners prevented us from sampling all colonies each year (e.g., Kokechik Bay 1992) and because encounter probabilities for marked brant were low at some colonies. We therefore combined observations from several colonies for some analyses and focused our effort on estimating movement probabilities for the Tutakoke River colony.

Brant at Tutakoke were banded in large numbers (>100) since 1986. At most other breeding colonies banding was not started until 1990. In addition, at Tutakoke,

encounters of brant occurred over 3 months (May-July) during 3 periods of the summer; observations during nesting (May and June) and brood rearing (early July), and recaptures during banding (late July). At other colonies, encounter probabilities were likely lower than at Tutakoke because observations generally occurred over a shorter time. Therefore, we estimated probabilities of natal philopatry and permanent emigration only for goslings banded at Tutakoke. We recorded natal dispesal of goslings from Kokechik Bay and Colville River/Prudhoe Bay to test for sex-specific differences in dispersal probabilities. We estimated breeding movements for the Tutakoke colony, and we combined encounters from Baird Inlet Island, Kokechik Bay, Kigigak Island, Colville River, and Prudhoe Bay to estimate breeding movements for brant from these colonies.

Natal philopatry and permanent emigration for goslings from Tutakoke

We estimated probability of natal philopatry for male and female brant banded as goslings at Tutakoke between 1986-1991. We defined natal philopatry (F_{ijk}) as the probability that a brant of sex k banded in the jth cohort (year of banding) returned and bred at Tutakoke at age i (i = 2, 3, ... 7). Probability of philopatry was therefore equal to 1 minus the sum of permanent emigration and temporary emigration. We estimated probability of philopatry as:

$$F_{ijk} = \frac{\frac{N_{ijk}}{p_t^{\cdot}}}{N_{jk}\prod_{t} s^{\circ}},$$

where N_{ijk} was the number of brant of sex k banded in the jth cohort encountered (reobserved or recaptured) at Tutakoke at age i, p_t^* was the probability of encounter at Tutakoke in year t, given a bird was breeding at Tutakoke in that year (Sedinger et al. in prep.), N_{jk} was the number of brant of sex k banded in the jth cohort, and $\prod_{S}^{t} s^{\circ}$ was the product of survival from banding until year t. p_t^* was estimated as:

$$p_t^* = (1-((1-p^n)(1-p^b)(1-p^r)) ,$$

where, p^n was the probability of detection during nesting, p^b was the probability of detection during brood rearing, and p^r was the probability of recapture during banding (Kendall and Nichols 1995). We assumed encounter probabilities for males were equal to estimates obtained for females (see Ward et al. in review). Estimates of s° were not biased by permanent emigration because these estimates were based on observations of brant at Tutakoke, wintering areas in Mexico, and fall and spring staging areas (Sedinger et al. in review, Ward et al. in review). Because Ward et al. (in review) reported no difference between survival probability of male and female brant >1 year old, we assumed first year s° (banding to following summer) for males was equal to estimates obtained for females (Sedinger et al. in review). First year s° between banding in 1991 and summer 1992 was estimated as the product of s° from banding 1991 to winter 1992 and winter 1991 to summer 1991 because we lacked estimates for the period winter 1992 to summer 1992 (Sedinger et al. in review).

We estimated variance of natal philopatry (Appendix 1) using the delta method

(Seber 1982) and program Derive (Software Warehouse 1993). We obtained variance and covariance estimates for p_t^* from Sedinger et al. (in prep.). Variance estimates for s° were obtained from Sedinger et al. (in review) and Ward et al. (in review). Covariance between p_t^* and s°, and s° of goslings and s° adults was 0 because these estimates were obtained from independent data sets. We assumed no covariance between s° for adults (Ward et al. in review).

As defined above, estimates of natal philopatry to Tutakoke equaled 1 minus the sum of the probability of permanent and temporary emigration from Tutakoke. Estimates of breeding propensity $(1 - \gamma_i)$ for brant from Tutakoke equal 1 minus the probability of temporary emigration from Tutakoke (Sedinger et al. in prep.). Therefore, we obtained estimates of permanent emigration at age *i* for female brant banded in the *j*th cohort at Tutakoke as:

$$D_{ijf} = 1 - \left(\frac{F_{ijf}}{(1 - \gamma_{if})} \right),$$

where, γ_i was the probability of temporary emigration by females from Tutakoke at age *i*. We estimated variance of permanent emigration with the delta method (Seber 1982). Covariance between probability of natal philopatry and temporary emigration was 0 because these estimates were based on independent data sets. We could not estimate probability of permanent emigration for males because estimates of breeding propensity were not currently available.

We used ANCOVA (PROC GLM, SAS Inst. Inc. 1990) to test for age- and cohort-specific trends in probability of natal philopatry and permanent emigration for females and probability of natal philopatry for males. To examine age-specific trends we defined an ANCOVA model with cohort as a fixed factor and age as a covariate. In the ANCOVA model used to examine cohort-specific trends, cohort was a covariate and age was the fixed factor. We included an age*cohort interaction term in all models to test for heterogeneity in the relationship between the covariate and independent variable. We restricted our analyses of age- and cohort-specific variation in natal philopatry and permanent emigration to cohorts with at least 3 age classes (i.e., 1986-1989 cohorts) or ages with at least 3 cohorts (i.e., ages 2-5). For all ANCOVAs we weighted dependent variables by the reciprocal of the variance of each value (Manly 1985:413-414), therefore, dependent variables with large variances received less weighting than dependent variables with small variances.

Natal dispersal among colonies

We recorded natal dispersal among colonies by mapping encounters of goslings banded at Tutakoke River (1986-1992), Kokechik Bay (1990 and 1991), and Colville River/Prudhoe Bay (North Slope colonies) (1990-1992). We tested the hypothesis that natal dispersal and philopatry were independent of sex with χ^2 test of independence (PROC FREQ, SAS Inst. Inc. 1990). We combined observations of dispersal and philopatry for all cohorts and all age classes for these tests.

Breeding philopatry and dispersal

We used multistate modeling and program MSSURVIV (Brownie et al. 1993) to estimate probability of breeding philopatry and dispersal for adult brant from 1990-1994. Multistate modeling uses capture-recapture/resighting data from marked individuals to obtain maximum likelihood estimates of encounter (recapture/resight), survival, and movement probabilities. Encounter probabilities (p_{tk}^{s}) were defined as the probability of recapture/resighting at colony (stratum) s in year t for brant of sex k. Estimates of survival (s_{tk}^{r}) and movement probability (Ψ_{tk}^{rs}) result from decomposition of transition probabilities, Φ_{tk}^{rs} (probability that brant of sex k is alive and at stratum s in year t+1, given a brant was alive and at stratum r in year t; Brownie et al. 1993). Decomposition of Φ_{tk}^{rs} assumes that s_{tk}^{r}, probability that a brant of sex k at stratum r in year t is alive and at any stratum in year t+1, depends on the stratum occupied in year t and not on the stratum occupied in year t+1. This assumption seems reasonable because brant arrive at the stratum occupied in year t+1 at the end of the annual period over which survival is estimated. Breeding philopatry (Ψ_{tk}^{rs}) for the kth sex of brant was defined as the probability of being at stratum s in year t+1 for brant that were at stratum r (r=s) in year t and had survived to year t+1. Breeding dispersal (Ψ_{tk}^{rs}) for the kth sex of brant was defined as the probability of being at stratum s in year t+1 for brant that were at stratum r ($r \neq s$) in year t and had survived to year t+1.

Based on sampling effort, we defined Tutakoke River as 1 stratum and all remaining colonies (Kigigak Island, Kokechik Bay, Baird Inlet Island, Prudhoe Bay, and

Colville River) as a single stratum. Estimates of breeding movements therefore reflect philopatry to Tutakoke and dispersal to any of the 5 breeding colonies listed previously, or philopatry to all of the 5 breeding colonies combined and dispersal to Tutakoke. Adult brant banded at breeding colonies before 1990 and adults banded at molting areas were included in our sample only if they were encountered at a breeding colony between 1990-1993. Breeding brant at the colonies included in our analyses account for approximately 80% of the estimated number of breeding pairs of black brant (Sedinger et al. 1993).

Our approach to parameter estimation and hypothesis testing was first to attempt to reduce sources of variation in encounter and survival probabilities thereby increasing power for hypothesis tests about movement probabilities (Lebreton et al. 1992). Therefore, we constructed models that constrained p^s_{tk} and s^r_{tk} equal over strata (p_{tk}, s_{tk}), years (p^s_k, s^r_k), sexes (p^s_t, s^r_t), combinations of these factors, and all possible sources of variation (p, s) (64 models). We used Akaike Information Criteria (AIC, Akaike 1992, Burnham and Anderson 1992) and χ^2 goodness-of-fit tests to select the most parsimonious model with p^s_{tk} and s^r_{tk} constraints that adequately explained these data. We maintained constraints on p^s_{tk} and s^r_{tk} to test specific hypotheses about movement probability. We tested for sex-, strata-, and year-specific variation in movement probabilities with AIC and likelihood ratio tests (LRT, Lebreton et al. 1992).

RESULTS

Natal philopatry and permanent emigration for goslings from Tutakoke

Probability of philopatry for goslings from Tutakoke River ranged from 0.39 to

0.97 for females and from 0.08 to 0.29 for males (Table 1). Estimates of permanent emigration for females were more variable, including estimates ranging from 0.0 to 0.44 (Table 2). We observed no evidence ($P > 0.07$) of heterogeneity in slopes in any of the ANCOVA models used to investigate the relationship between natal philopatry or permanent emigration and age or cohort effects. Therefore, interaction terms were removed from the models. Probability of natal philopatry for females increased with age ($t = 3.77$, df = 1, $P = 0.002$; Fig. 2). We observed a significant decline in probability of natal philopatry of females with cohort ($t = -2.45$, df = 1, $P = 0.029$; Fig. 3). In contrast, we observed no evidence of a relationship between the probability of natal philopatry for males and age ($t = 1.46$, df = 1, $P = 0.169$; Fig. 4) or cohort ($t = 0.67$, df = 1, $P = 0.512$; Fig. 5). Probability of permanent emigration for females increased with age ($t = 2.45$, df =1, $P = 0.030$; Fig. 2) and cohort ($t = 2.79$, df =1, $P = 0.015$) (Fig. 3).

Natal dispersal among colonies

Male ($n = 4,070$) and female ($n = 4,076$) goslings banded at Tutakoke River between 1986-1992 were encountered (1990-1994) at all breeding colonies on the Yukon-Kuskokwim River Delta, including 1 female observed at a small colony (<100 pairs) near the mouth of the Manokinak River, Alaska (Fig. 6). Male goslings banded at Kokechik Bay (1990-1991) ($n = 324$) and North Slope colonies (1990-1992) ($n = 553$) were encountered at all breeding colonies that we sampled between 1992-1994, except Baird Inlet Island, which was sampled only in 1992 (Fig. 6). The only natal dispersal recorded for female goslings banded at Kokechik Bay (n = 302) or North Slope colonies ($n = 525$)

was movement to the Tutakoke River colony. Natal dispersal and philopatry were not independent of sex. Female goslings from all 3 colonies were significantly more likely to exhibit philopatry (Tutakoke River, $\chi^2 = 91.9$, 1 df, $P = 0.001$; Kokechik Bay, $\chi^2 = 3.9$, 1 df, $P = 0.047$; North Slope colonies, $\chi^2 = 10.2$, 1 df, $P = 0.001$) than male goslings.

Breeding philopatry and dispersal

We obtained 9,565 encounters of 5,545 adult female brant and 7,309 encounters of 4,752 adult male brant (Table 3). Most (>77%) encounters occurred at the Tutakoke River colony. Of the 64 models that constrained encounter and survival probabilities, only 2 models have AIC values <547. These models were similar, both models had sex-, strata-, and year-specific survival probabilities. One model (model A, AIC = 512) had no constraints on encounter probabilities. The other model (model B, AIC = 510) constrained encounter probabilities equal over sexes. Because AIC was lower for model B and the LRT between models A and B failed to reject ($\chi^2 = 9.57$, 6 df, $P = 0.14$) the reduced model (i.e., model B), we maintained model B constraints for further tests about movement probabilities.

Probability of philopatry was constant between sexes ($\chi^2 = 35.8$, 8 df, $P < 0.001$), between strata ($\chi^2 = 280.7$, 8 df, $P < 0.001$), or among years ($\chi^2 = 54.2$, 12 df, $P < 0.001$). Therefore, we used the most general model (i.e., movement probabilities vary by year, sex, and strata; model B) to obtain estimates of encounter, survival (Table 4), and movement probabilities (general model goodness-of-fit test without pooling, $\chi^2 = 103$, 122 df, $P = 0.89$). Breeding philopatry was high (>0.91) for both females and males (Fig. 7).

Probability of philopatry for females was higher (i.e., LRT between general model and model with movement probabilities equal between sexes, $\chi^2 = 36$, 8 df, $P < 0.001$) than probability of philopatry for males except for other colonies in 1993.

DISCUSSION

Estimators of philopatry and dispersal

Return rate (i.e., product of survival, capture probability, and homing) is the most commonly reported parameter in estimates of philopatry for avian populations. Although return rates may be used to draw tentative conclusions about philopatry (Johnson et al. 1992), sex-specific survival probabilities and temporal and geographic variation in capture probabilities may produce biased estimates (Martin et al. 1995). Homing rates (i.e., product of capture probability and homing, see Lokemoen 1990) may be estimated if survival probability is known; however, comparison of homing rates over time or among regions is tenuous because of the potential for temporal and regional variation in capture probability.

If estimates of 'true' survival (e.g., survival estimates not biased by permanent emigration) and 'apparent' survival (e.g., survival estimates that reflect both mortality and permanent emigration) are available (e.g., Francis and Cooke 1993), then 1 minus ratio of apparent:true survival provides an estimate of probability of permanent emigration (Johnson et al. 1992). The ratio, apparent to true survival, has been used as an estimate of philopatry (Anderson and Sterling 1974, Hepp et al. 1987, see also Szymczak and Rexstad 1991, Blums et al. 1996); however, this estimator is based on the assumption of no

temporary emigration. This assumption may be valid for mature birds or populations with 100% breeding propensity. If temporary emigration is >0 then the ratio apparent to true survival will overestimate probability of philopatry by the amount of temporary emigration, potentially leading to biased estimates of apparent survival (Burnham 1993). Thus, use of this estimator may therefore be misleading for populations exhibiting delayed maturation or variation in breeding propensity.

The *ad hoc* estimator of philopatry used in this study accounts for both permanent and temporary emigration. Although the estimator has a simplistic form, we recognize that many parameters (e.g., local capture probabilities and true survival probabilities) are needed to obtain estimates of philopatry. As a result, variance estimators are complex and movement estimates for older brant were less precise. Theoretically, more direct estimates of both permanent and temporary emigration and associated variances should be possible by explicitly modeling the capture-recapture process (e.g., Burnham 1993, Kendall and Nichols 1995). If sampling protocols include recaptures of both temporary and permanent emigrants then multistate modeling (Brownie et al. 1993) should provide estimates of philopatry, permanent emigration, and temporary emigration (Nichols et al. 1994, Nichols and Kendall 1995). For example, the sampling protocol used in this study could have been expanded to include more extensive sampling of breeding colonies and molting areas (e.g., Teshekpuk Lake, Alaska, see Bollinger and Derksen 1996) used by temporary emigrants.

Female-biased philopatry

Similar to previous studies of waterfowl populations (Greenwood 1980,

Greenwood and Harvey 1982, Rohwer and Anderson 1988, Anderson et al. 1992), we observed strong evidence that philopatry in brant was female biased. Breeding dispersal by female brant was rare (probability <0.06) and long-term monogamy, which is common in most geese (Owen 1980), was probably the cause of relatively high rates of breeding philopatry for male brant. We suspect that breeding philopatry of males was generally lower than females because of males pairing with females from other colonies following loss of a mate (see Cooke et al. 1975, Lessels 1985). Our estimates of breeding philopatry for both male and female brant were higher than estimates of return rates previously reported for waterfowl (Anderson et al. 1992, Table 11-3) and estimates of homing rates reported for several species of ducks (Lokemoen et al. 1990). Our estimates of breeding philopatry were similar to estimates based on ratios of apparent to true survival reported for several duck species (Hepp et al. 1987, see also Szymczak and Rexstad 1991, Blums et al. 1996). Similarly, the ratio of apparent to true survival (Sedinger et al. in review, Ward et al. in review) for adult brant is approximately 1.00.

Estimates of natal philopatry exhibited even stronger evidence of female bias. Probability of philopatry for female brant from Tutakoke was approximately 5 times as high as probability of male philopatry for brant >4 years old. Female brant from Kokechik Bay and North Slope colonies were significantly more likely to exhibit natal philopatry than males from these colonies.

Female-biased philopatry in waterfowl is almost unique among birds (Greenwood 1980). We favor the mating-system hypothesis proposed by Greenwood (1980) and

developed by Rohwer and Anderson (1988) to explain patterns of male-biased dispersal in brant. Furthermore, we suspect that low probabilities of natal philopatry reported for previous studies of male geese, which favor an inbreeding-avoidance hypothesis (Anderson et al. 1992), may reflect biases in estimation techniques and underestimate true probabilities of philopatry for males. Probability of inbreeding in brant is greatly reduced by weak family integrity (Jones and Jones 1966), coupled with pair formation on wintering areas (Greenwood 1987, Rohwer and Anderson 1988). If inbreeding avoidance is an important factor determining probability of philopatry, then negative assortative mating (Greenwood et al. 1978) would lead to a lower probability of natal philopatry for males than predicted under a model of random pairing relative to the colony of origin. In contrast, positive assortative mating would result in a higher probability of natal philopatry for males than predicted under a hypothesis of random mating (Rockwell and Barrowclough 1987).

Expected probability of male philopatry under a hypothesis of random mating is probability that a male pairs with a female that returns to his natal colony. Based on current estimates of number of breeding pairs at Tutakoke River (Sedinger et al. 1993), we estimated that unpaired females from Tutakoke account for approximately 22% of the unpaired females in the entire population. Additionally, probability of natal philopatry for females from Tutakoke is about 0.75 (Fig. 2). Based on estimates of permanent emigration by females from Tutakoke (ca. 0.25, Table 2), we expect that probability of immigration to Tutakoke is approximately 0.06 (0.25*0.22). Therefore, expected

probability of natal philopatry for males born at Tutakoke is; (0.22*0.75) + (0.78*0.06) = 0.21. Admittedly, these calculations are crude, and we lack a direct test of differences in expected and observed probabilities of natal philopatry for males. Observed probabilities of natal philopatry of males, however, are similar to those predicted under a model of random mating. Like Cooke et al. (1995), we suspect that deviations from a model of random mating may result from nonrandom mixing of populations on wintering areas.

Age- and density-dependent effects

Probability of natal philopatry of females was higher for older brant because probability of temporary emigration declined with age (Sedinger et al. in prep.). We observed no evidence that probability of natal philopatry for males increased with age, suggesting that temporary emigration is less prevalent in males than do females. We currently lack analyses of breeding propensity of male brant; however, observations of yearling Lesser Snow Geese (*Anser caerulescens caerulescens*) suggest that males may pair or associate with potential mates sooner than females (Cooke et al. 1995). That is, fewer yearling males return to breeding areas with their parents than yearling females (Cooke et al. 1995).

We did not anticipate an age-related increase in probability of permanent emigration for females because we assumed this form of emigration was permanent during the study. Estimates of breeding propensity were constrained equal for brant 5 to 7 years old (Sedinger et al. in prep.), which may have reduced the accuracy of estimates of permanent emigration for brant >5 years old. Within cohorts (1986 and 1987), estimates

of permanent emigration for brant >5 years old were among the highest. We therefore suggest that age-related increases in permanent emigration reflect lack of cohort-specific estimates of breeding propensity.

The cohort-specific increase in probability of permanent emigration and decrease in probability of natal philopatry of females corresponded to a period of increasing colony size at Tutakoke. Between 1986 and 1992, number of brant nesting at Tutakoke increased from 1,100 pairs to approximately 6,100 pairs (Sedinger et al. 1993). During this period, within-colony dispersal of brant from natal nest sites has resulted in an expansion of the colony (Lindberg et al. in prep.), and we suspect increased competition for nest sites. Effects of density on movement probabilities have been observed in other avian populations. Habitat degradation caused by increased population size may increase probability of dispersal from traditional brood rearing sites in Snow Geese (Cooch et al. 1993). Male Great Tits (*Parus major*) disperse farther as population density increases (Greenwood et al. 1979). Like Spendelow et al. (1995), our data do not support McPeek and Holt's (1992) prediction of an inverse relationship between colony size and probability of dispersal.

Density-dependent trends in probability of permanent emigration and natal philopatry may be caused by 3 demographic changes; reduced breeding propensity (e.g., delays in breeding), increased dispersal from Tutakoke, and increased probability of permanent nonbreeding. Sedinger et al. (in prep.) observed no cohort-specific variation in breeding propensity, and we therefore have no evidence that increased density reduced

breeding propensity. Our estimates of permanent emigration suggest that natal dispersal among colonies has increased; however, we could not always distinguish natal dispersal (i.e., emigration and breeding) from permanent nonbreeding (i.e., emigration and non-breeding). We reduced the probability of including nonbreeding individuals in our sample of emigrants by eliminating observations of 1-year-old brant and observations of brant seen at >1 colony during a summer. We determined breeding status of emigrants based on behavior (e.g., territorial males) or more directly by locating the nest of marked brant. Based on these criteria, we confirmed that 47 and 60% of the females and males, respectively, observed as emigrants from Tutakoke River were breeding at the other colonies. Breeding by emigrants from Kokechik Bay and North Slope colonies was confirmed for 43 and 44% of the individuals, respectively.

Observed number of female emigrants from Tutakoke was less than the expected number even if we assumed that all emigrants were breeding at recipient colonies. For example, number of females from the 1989 Tutakoke cohort expected to be seen at other colonies (Kokechik, Colville, Prudhoe, Baird Inlet, Kigigak) in 1991 equals the product of number of female goslings banded at Tutakoke in 1989 (705) x survival probability to 1991 (0.57) x probability of permanent emigration from Tutakoke (0.185) x breeding propensity of 2 year old brant (0.613, Sedinger et al. in prep) x encounter probability at other colonies in 1991 (0.135, Table 4) x proportion of breeding pairs at other colonies relative to total breeding population of brant (0.63, Sedinger et al. 1993). The expected number for this example was 4; however, only 2 female emigrants were observed and the

breeding status of 1 of these individuals was unknown. Total number of expected emigrants (1991-1993) for all cohorts (1986-1991) was 53 females, but only 12 were observed. These individuals may have dispersed to breeding colonies that we did not sample; however, our sampling included about 80% of the breeding populations and we detected no female emigrants at Anderson River, N.W.T., Canada in 1992. We therefore suspect that permanent nonbreeding or extreme delays (beyond age 5) in age of first reproduction contributed to observed trends in permanent emigration and natal philopatry. More data on the age structure of nonbreeding brant using molting areas are required to resolve this question. Increased probability of permanent emigration may not reflect increased levels of gene flow from Tutakoke.

In contrast to females, we observed no cohort specific variation in probability of natal philopatry of males. Decline in natal philopatry of males should not be as steep as the decline in female philopatry because pairing with a female that is philopatric to Tutakoke accounts for only about 80% of the males that return to Tutakoke (see above). Pairing with females that immigrate to Tutakoke accounts for the other 20% of males exhibiting philopatry to Tutakoke. We currently lack adequate data to explain differences in the pattern of natal philopatry of males and females.

Gene flow and genetic structure

Effects of gene flow on the genetic structure of populations are difficult to quantify, as the homogenizing influence of gene flow is counterbalanced by the diversifying forces of genetic drift, mutation, and natural selection (Mayr 1942). For avian

populations, indirect and direct measures of genetic population structure generally indicate a small component of among-population genetic variance, therefore implying high rates of gene flow (Barrowclough 1980, Barrowclough 1983, Rockwell and Barrowclough 1987). More specifically, estimates of gene flow based on direct observations of marked Lesser Snow Geese indicate that male-mediated gene flow among Snow Goose populations is extensive and allelic frequencies among populations are nearly equal (Cooke et al. 1975, Rockwell and Cooke 1977, Rockwell and Barrowclough 1987). Avise et al. (1992) and Quinn (1992), however, showed a lack of geographic localization for distinct mitochondrial DNA (Gyllensten et al. 1985), in Snow Geese despite high probabilities of female philopatry (Cooke et al. 1995). Avise et al. (1992) and Quinn et al. (1992) therefore cautioned that contemporary estimates of gene flow may not reflect evolutionary components of population relatedness; genetic markers can provide misleading estimates of contemporary levels of gene flow because they retain a record of historical events. Other studies of goose populations have shown distinct mtDNA types for subspecies and geographically isolated populations of Canada geese (*Branta canadensis sp.*) (Shields and Wilson 1987, Van Wagner and Baker 1990, Shields 1996) implying low probabilities of female-mediated gene flow among populations.

Based on restriction fragment analysis of mtDNA, Shields (1990) demonstrated extensive divergence between Black Brant and Atlantic Brant (*B. b. hrota*) and Black Brant and "gray-bellied" brant nesting on Melville Island, N.W.T., Canada. His analyses included 4 populations of Black Brant that showed essentially identical mtDNAs (Shields

1990) and may indicate dispersal of females among populations or recent evolutionary relatedness of black brant populations. Use of more informative DNA amplification and sequencing of specific mtDNA segments suggest colony specific markers may occur in the mitochondrial genome of black brant (Shields, unpubl. data). We are currently sequencing control regions of mtDNA from 3 brant populations. We plan to compare direct and indirect measures of gene flow for brant in future analyses and therefore obtain a more thorough view of contemporary levels of gene flow and evolutionary connectedness of brant populations.

Our estimates of male philopatry do not indicate that positive assortative mating is prevalent in brant. That is, observed probability of natal philopatry for males is similar to probability of philopatry expected under a model of random pairing relative to colony of origin. Our findings are in contrast to observational and genetic studies of Atlantic Brant, which suggest that separation of breeding populations in wintering areas and mate selection based on morphological characteristics may lead to assortative mating (Abraham et al. 1983, Vangilder and Smith 1985, Novak et al. 1989). Although temporal and geographic separation of brant populations has been observed during the nonbreeding season (Reed et al. 1989a & b), more detailed studies of brant wintering in Mexico are needed to clearly understand the extent of population mixing during a potential important time for pair formation.

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Table 1. Estimated probability of philopatry to the Tutakoke River colony, Alaska 1988-1993 for female and male goslings banded at Tutakoke 1986-1991 (cohort). Standard error estimates are shown in parentheses.

			Age					
Cohort	n[a]	Sex	2	3	4	5	6	7
1986	140	F	0.482 (0.106)	0.675 (0.164)	0.777 (0.196)	0.812 (0.229)	0.757 (0.238)	0.775 (0.307)
	146	M	0.084 (0.019)	0.174 (0.042)	0.277 (0.070)	0.182 (0.051)	0.290 (0.091)	0.203 (0.080)
1987	587	F	0.597 (0.075)	0.743 (0.105)	0.915 (0.173)	0.967 (0.226)	0.724 (0.244)	
	571	M	0.156 (0.019)	0.175 (0.025)	0.205 (0.039)	0.191 (0.045)	0.167 (0.056)	
1988	495	F	0.514 (0.048)	0.551 (0.086)	0.730 (0.152)	0.529 (0.169)		
	498	M	0.131 (0.012)	0.221 (0.033)	0.226 (0.047)	0.120 (0.038)		
1989	705	F	0.576 (0.078)	0.624 (0.120)	0.558 (0.172)			
	753	M	0.182 (0.025)	0.179 (0.034)	0.094 (0.029)			
1990	726	F	0.490 (0.101)	0.400 (0.125)				
	699	M	0.146 (0.030)	0.157 (0.049)				
1991	754	F	0.386 (0.108)					
	755	M	0.120 (0.033)					

[a] n denotes number of goslings banded in each cohort.

Table 2. Estimated probabiltiy of permanent emigration from Tutakoke River, Alaska 1988-1993 for female goslings banded at Tutakoke 1986-1991. Standard error estimates are shown in parentheses.

		Age					
Cohort	n[a]	2	3	4	5	6	7
1986	140	0.210 (0.176)	0.049 (0.235)	0.133 (0.223)	0.141 (0.243)	0.199 (0.252)	0.180 (0.325)
1987	587	0.021 (0.129)	-0.046 (0.155)	-0.021 (0.200)	-0.023 (0.241)	0.234 (0.258)	
1988	495	0.157 (0.086)	0.224 (0.126)	0.185 (0.174)	0.440 (0.179)		
1989	705	0.056 (0.133)	0.121 (0.173)	0.377 (0.195)			
1990	726	0.197 (0.168)	0.437 (0.178)				
1991	754	0.367 (0.178)					

[a] n denotes number of goslings banded in each cohort.

Table 3. Number of adult female and male brant encountered (sighted/captured) at Tutakoke River, Alaska and other (Kigigak Island, Kokechik Bay, Baird Inlet Island, Prudhoe Bay, and Colville River; Alaska) colonies 1990-1994.

		Encounter Location	
Year	Sex	Tutakoke	Other
1990	F	1,403	283
	M	1,000	280
1991	F	1,598	563
	M	1,165	512
1992	F	1,905	380
	M	1,341	385
1993	F	1,781	642
	M	1,307	589
1994	F	901	109
	M	555	75

Table 4. Estimated encounter ($\hat{p}_t^s$) and survival ($\hat{S}_{tk}^r$) probabilities for adult female and male brant, Tutakoke River, Alaska and other colonies (Kigigak Island, Kokechik Bay, Baird Inlet Island, Prudhoe Bay, and Colville River; Alaska), 1990-1994. Standard error estimates are presented in parentheses.

		$\hat{p}_t^s$		$\hat{S}_{tk}^r$	
Year	Sex	Tutakoke	Other	Tutakoke	Other
1990	F			0.800 (0.017)	0.650 (0.085)
	M			0.762 (0.024)	0.611 (0.087)
1991	F	0.583 (0.014)	0.135 (0.022)	0.841 (0.017)	0.982 (0.113)
	M			0.777 (0.025)	1.000 (0.128)
1992	F	0.640 (0.013)	0.052 (0.007)	0.739 (0.021)	0.441 (0.058)
	M			0.624 (0.022)	0.345 (0.048)
1993[a]	F	0.547 (0.015)	0.349 (0.039)	0.344 (0.011)	0.118 (0.012)
	M			0.308 (0.012)	0.084 (0.010)

[a] Survival probability estimates for 1993 are the product of survival between 1993 and 1994 and encounter probabilities for 1994.

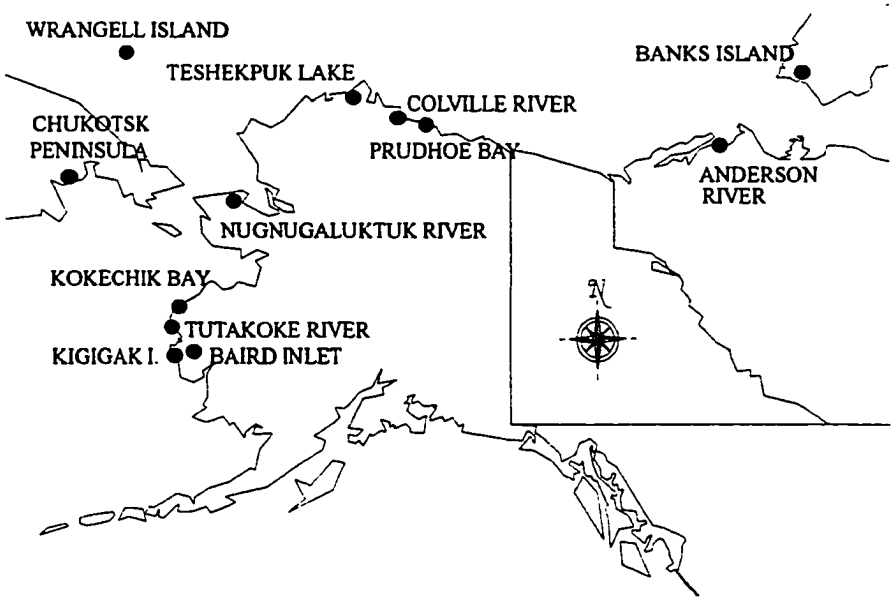

Figure 1. Locations of major breeding colonies and molting areas of black brant.

Breeding colony on Victoria Island, N.W.T., Canada is not shown.

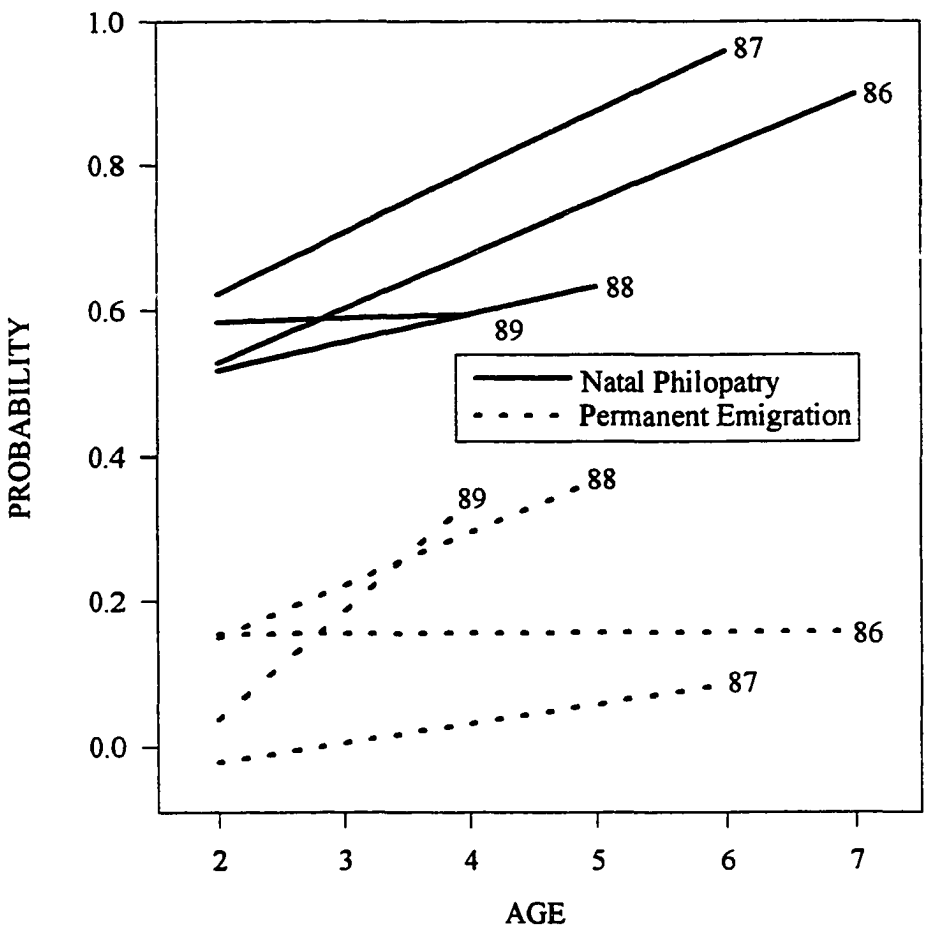

Figure 2. Relationship between age and probability of natal philopatry and permanent emigration for female brant hatched at Tutakoke River, Alaska (1986-1989). Numbers at end of each line represent year of banding (cohort).

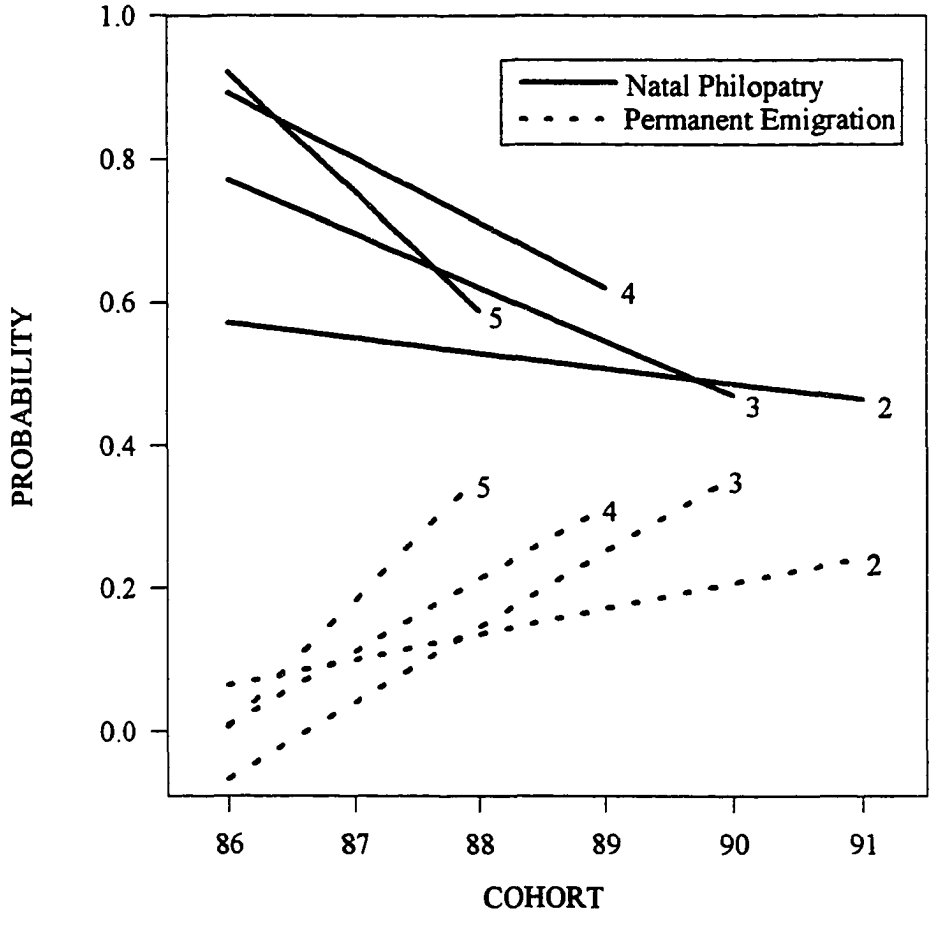

Figure 3. Relationship between year of banding (cohort) and probability of natal philopatry and permanent emigration for female brant hatched at Tutakoke River, Alaska (1986-1989). Numbers at end of each line represent the age of the brant.

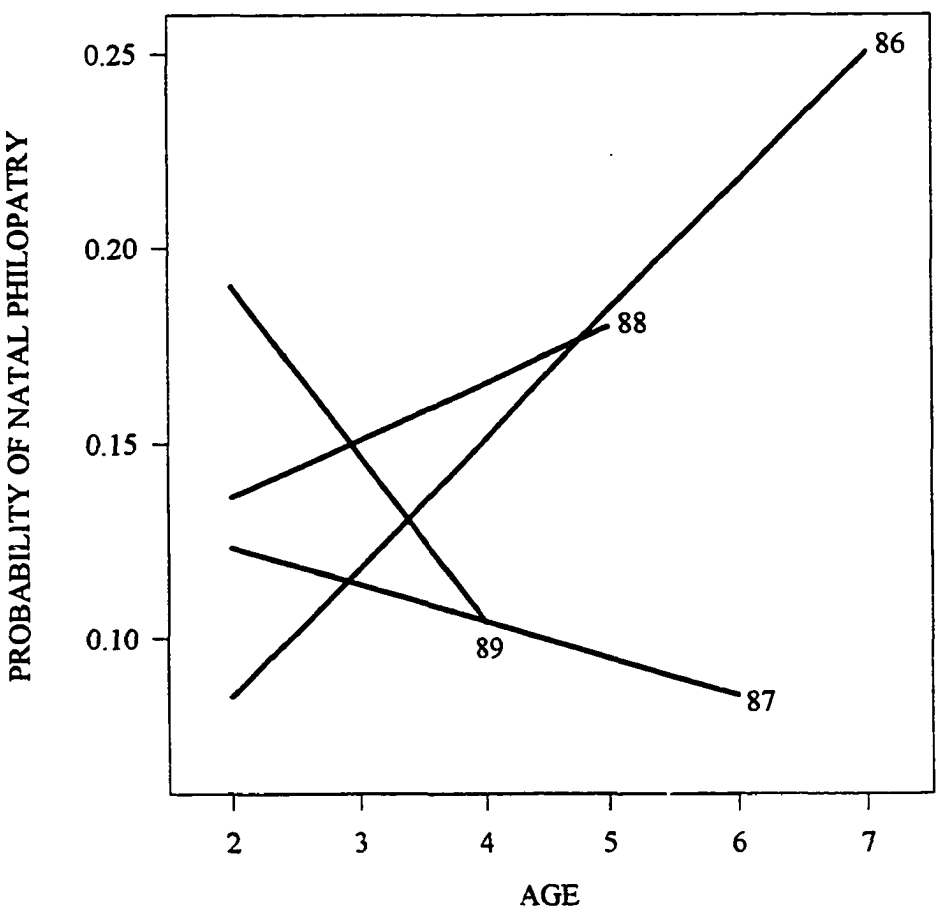

Figure 4. Relationship between age and probability of natal philopatry for male brant hatched at Tutakoke River, Alaska (1986-1989). Numbers at end of each line represent year of banding (cohort).

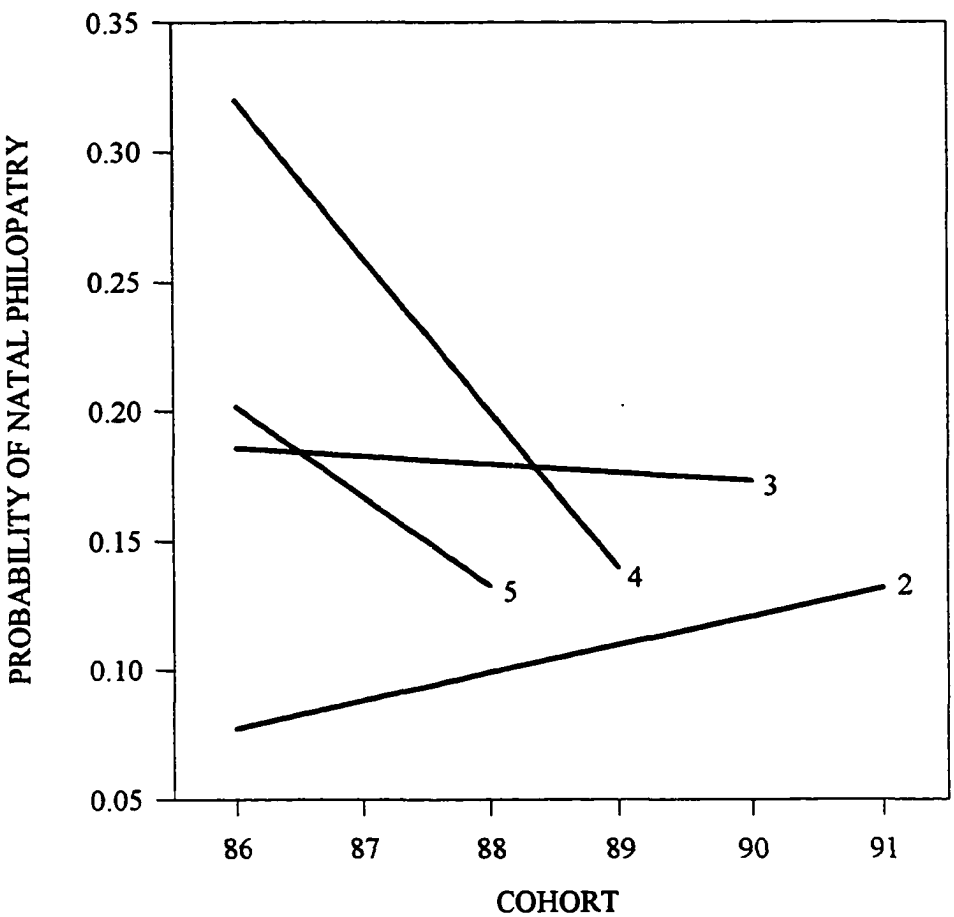

Figure 5. Relationship between year of banding (cohort) and probability of natal philopatry for male brant hatched at Tutakoke River, Alaska (1986-1989). Numbers at end of each line represent the age of the brant.

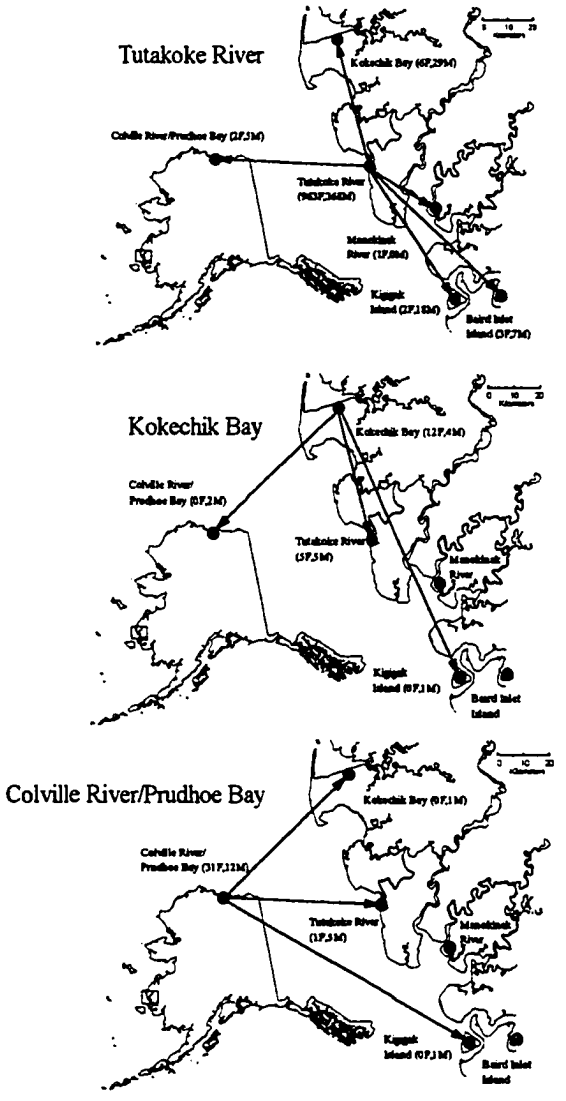

Figure 6. Observations of natal philopatry and dispersal for brant banded at the Tutakoke River (1986-1992, n = 4,076 F, n = 4,070 M), Kokechik Bay (1990-1991, n = 302 F, n = 324 M), and Colville River/Prudhoe Bay (1990-1992, n = 525 F, n = 553 M) colonies, Alaska. Numbers in parentheses are number of individual female (F) and male (M) brant seen at each colony between 1990-94 for brant banded at Tutakoke and between 1992-1994 for brant banded at Kokechik Bay and Colville River/Prudhoe Bay.

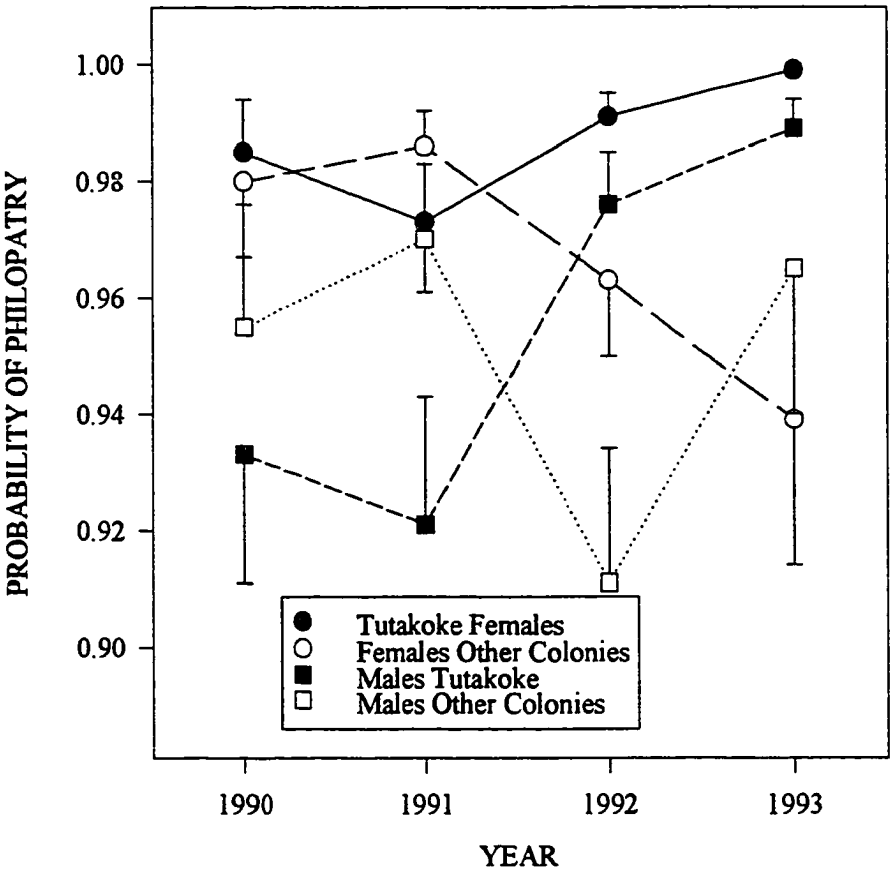

Figure 7. Estimated probability of breeding philopatry (1990-1993) for female and male brant, Tutakoke River, Alaska and other colonies (Kokechik Bay, Baird Inlet Island, Kigigak Island, Colville River, and Prudhoe Bay, Alaska). Bars represent standard errors of estimates.

APPENDIX 1.

Variance of philopatry for 2 year old brant ($\hat{var}(F_2)$) was estimated as:

$$\hat{var}(F_2) = N_i^2(2\hat{cov}(p_n p_b)\hat{S}_g^2\hat{S}_a^2(\hat{p}_r - 1)^2(\hat{p}_b - 1)(\hat{p}_n - 1) + 2\hat{cov}(p_n p_r)\hat{S}_g^2\hat{S}_a^2$$
$$(\hat{p}_r - 1)(\hat{p}_b - 1)^2(\hat{p}_n - 1) + 2\hat{cov}(p_n S_g)\hat{S}_g\hat{S}_a^2(\hat{p}_r - 1)(\hat{p}_b - 1)(\hat{p}_n(\hat{p}_r - 1)(\hat{p}_b - 1) +$$
$$\hat{p}_b(1 - \hat{p}_r) + \hat{p}_r) + 2\hat{cov}(p_n S_a)\hat{S}_g^2\hat{S}_a(\hat{p}_r - 1)(\hat{p}_b - 1)(\hat{p}_n(\hat{p}_r - 1)(\hat{p}_b - 1) +$$
$$\hat{p}_b(1 - \hat{p}_r) + \hat{p}_r) + 2\hat{cov}(p_b p_r)\hat{S}_g^2\hat{S}_a^2(\hat{p}_r - 1)(\hat{p}_b - 1)(\hat{p}_n - 1)^2 +$$
$$2\hat{cov}(p_b S_g)\hat{S}_g\hat{S}_a^2(\hat{p}_r - 1)(\hat{p}_n(\hat{p}_r - 1)(\hat{p}_b - 1) + \hat{p}_b(1 - \hat{p}_r) + \hat{p}_r)(\hat{p}_n - 1) +$$
$$2\hat{cov}(p_b S_a)\hat{S}_g^2\hat{S}_a(\hat{p}_r - 1)(\hat{p}_n(\hat{p}_r - 1)(\hat{p}_b - 1) + \hat{p}_b(1 - \hat{p}_r) + \hat{p}_r)(\hat{p}_n - 1) +$$
$$2\hat{cov}(p_r S_g)\hat{S}_g\hat{S}_a^2(\hat{p}_b - 1)(\hat{p}_n(\hat{p}_r - 1)(\hat{p}_b - 1) + \hat{p}_b(1 - \hat{p}_r) + \hat{p}_r)(\hat{p}_n - 1) +$$
$$2\hat{cov}(p_r S_a)\hat{S}_g^2\hat{S}_a(\hat{p}_b - 1)(\hat{p}_n(\hat{p}_r - 1)(\hat{p}_b - 1) + \hat{p}_b(1 - \hat{p}_r) + \hat{p}_r)(\hat{p}_n - 1) +$$
$$2\hat{cov}(S_g S_a)\hat{S}_g\hat{S}_a(\hat{p}_n(\hat{p}_r - 1)(\hat{p}_b - 1) + \hat{p}_b(1 - \hat{p}_r) + \hat{p}_r)^2 + \hat{p}_n^2(\hat{p}_b^2(\hat{p}_r^2(\hat{S}_g^2\hat{var}(S_a) +$$
$$\hat{S}_a^2\hat{var}(S_g)) - 2\hat{p}_r(\hat{S}_g^2\hat{var}(S_a) + \hat{S}_a^2\hat{var}(S_g))$$
$$+ \hat{S}_g^2(\hat{S}_a^2\hat{var}(p_r) + \hat{var}(S_a)) + \hat{S}_a^2\hat{var}(S_g)) -$$
$$2\hat{p}_b(\hat{p}_r^2(\hat{S}_g^2\hat{var}(S_a) + \hat{S}_a^2\hat{var}(S_g)) - 2\hat{p}_r(\hat{S}_g^2\hat{var}(S_a) + \hat{S}_a^2\hat{var}(S_g)) + \hat{S}_g^2(\hat{S}_a^2\hat{var}(p_r) +$$
$$\hat{var}(S_a)) + \hat{S}_a^2\hat{var}(S_g)) + \hat{p}_r^2(\hat{S}_g^2(\hat{S}_a^2\hat{var}(p_b) + \hat{var}(S_a)) + \hat{S}_a^2\hat{var}(S_g)) -$$
$$2\hat{p}_r(\hat{S}_g^2(\hat{S}_a^2\hat{var}(p_b) + \hat{var}(S_a)) + \hat{S}_a^2\hat{var}(S_g)) + \hat{S}_g^2(\hat{S}_a^2(\hat{var}(p_b) + \hat{var}(p_r)) + \hat{var}(S_a)) +$$
$$\hat{S}_a^2\hat{var}(S_g)) - 2\hat{p}_n(\hat{p}_b^2(\hat{p}_r^2(\hat{S}_g^2\hat{var}(S_a) + \hat{S}_a^2\hat{var}(S_g)) - 2\hat{p}_r(\hat{S}_g^2\hat{var}(S_a) + \hat{S}_a^2\hat{var}(S_g)) +$$
$$\hat{S}_g^2(\hat{S}_a^2\hat{var}(p_r) + \hat{var}(S_a)) + \hat{S}_a^2\hat{var}(S_g)) - \hat{p}_b(2\hat{p}_r^2(\hat{S}_g^2\hat{var}(S_a) + \hat{S}_a^2\hat{var}(S_g)) -$$
$$3\hat{p}_r(\hat{S}_g^2\hat{var}(S_a) + \hat{S}_a^2\hat{var}(S_g)) + \hat{S}_g^2(2\hat{S}_a^2\hat{var}(p_r) + \hat{var}(S_a)) + \hat{S}_a^2\hat{var}(S_g)) +$$
$$\hat{p}_r^2(\hat{S}_g^2(\hat{S}_a^2\hat{var}(p_b) + \hat{var}(S_a)) + \hat{S}_a^2\hat{var}(S_g)) - \hat{p}_r(\hat{S}_g^2(2\hat{S}_a^2\hat{var}(p_b) + \hat{var}(S_a)) +$$
$$\hat{S}_a^2\hat{var}(S_g)) + \hat{S}_g^2\hat{S}_a^2(\hat{var}(p_b) + \hat{var}(p_r))) +$$
$$\hat{p}_b^2(\hat{p}_r^2(\hat{S}_g^2(\hat{S}_a^2\hat{var}(p_n) + \hat{var}(S_a)) + \hat{S}_a^2\hat{var}(S_g)) -$$
$$2\hat{p}_r(\hat{S}_g^2(\hat{S}_a^2\hat{var}(p_n) + \hat{var}(S_a)) + \hat{S}_a^2\hat{var}(S_g)) + \hat{S}_g^2(\hat{S}_a^2(\hat{var}(p_n) + \hat{var}(p_r)) + \hat{var}(S_a)) +$$
$$\hat{S}_a^2\hat{var}(S_g)) - 2\hat{p}_b(\hat{p}_r^2(\hat{S}_g^2(\hat{S}_a^2\hat{var}(p_n) + \hat{var}(S_a)) + \hat{S}_a^2\hat{var}(S_g)) - \hat{p}_r(\hat{S}_g^2(2\hat{S}_a^2\hat{var}(p_n) +$$
$$\hat{var}(S_a)) + \hat{S}_a^2\hat{var}(S_g)) + \hat{S}_g^2\hat{S}_a^2(\hat{var}(p_n) + \hat{var}(p_r))) + \hat{p}_r^2(\hat{S}_g^2(\hat{S}_a^2(\hat{var}(p_n) + \hat{var}(p_b)) +$$

$\hat{var}(S_a)) + \hat{S}_a^2 \hat{var}(S_g)) - 2\hat{p}_r \hat{S}_g^2 \hat{S}_a^2 (\hat{var}(p_n) + \hat{var}(p_b)) + \hat{S}_g^2 \hat{S}_a^2 (\hat{var}(p_n) + \hat{var}(p_b) + \hat{var}(p_r)))/(N^2 \hat{S}_g^4 \hat{S}_a^4 (\hat{p}_n(\hat{p}_r - 1)(\hat{p}_b - 1) + \hat{p}_b(1 - \hat{p}_r) + \hat{p}_r)^4)$;

where, $\hat{p}_n$ was the probability of detection at Tutakoke during nesting given a bird was present, $\hat{p}_b$ was the probability of detection at Tutakoke during brood rearing given a bird was present, $\hat{p}_r$ was the probability of recapture at Tutakoke during banding given a bird was present, $\hat{S}_g$ was survival probability of gosling from banding to the next summer, $\hat{S}_a$ was survival probability for brant between their first and second summer, N was the number of brant banded as goslings, and N_i was the number of brant banded as goslings seen in year i. Survival probabilities are estimated for the superpopulation and are therefore not biased by permanent emigration. Estimated variance of parameter X and covariance of parameters XY are represented as $\hat{var}(X)$ and $\hat{cov}(XY)$. Estimated variance of philopatry for brant >2 years old include additional survival probability estimates and associated variances and covariances.

OVERALL CONCLUSIONS

Nest-Site Fidelity and Nesting Phenology: Female brant exhibited high probabilities (>0.72) of fidelity to previous nest sites. Distribution of dispersal distances was highly leptokurtic. Nest success, spring environment, and age affected nest site fidelity. Female brant that experienced partial or complete loss of a clutch dispersed farther than females that experienced no loss of eggs. My results are consistent with previous studies of avian populations that demonstrated a relationship between nest success and future probability of site fidelity (e.g., Greenwood et al. 1979, Dow and Fredga 1983, Burger et al. 1982, Gavin and Bollinger 1988, Lokemoen et al. 1990, Majewski and Beszterda 1990).

Spring environment (snow conditions) affected not only site fidelity of brant, but also nesting phenology and clutch size. Brant delayed nesting in late springs, but also nested sooner relative to phenology of spring snowmelt in these years. Brant therefore maintained a consistent interval between arrival and timing of nest initiation. Proximity of spring staging areas to breeding areas on tne Yukon-Kuskokwim River Delta may allow brant to accurately predict snowmelt on breeding grounds. Unlike previous studies of waterfowl populations that documented reduced clutches in late spring (Barry 1962, Raveling 1978, Dau and Mickelson 1979, Ely and Raveling 1984, MacInnes and Dunn 1988) or no relationship between spring environment and clutch size (Bruggink et al. 1994), clutch size of brant was greater in late springs than early springs suggesting reduced breeding propensity by younger brant in late springs or increased body condition

resulting from increased time spent on spring staging areas Brant may disperse from traditional nest sites in late springs, but appear to return to these sites in subsequent breeding attempts. Dispersal from nest sites in late springs is probably a strategy to maintain earliest possible nest initiation because timing of hatch affects subsequent growth, survival, and fecundity of goslings (Sedinger and Flint 1991, Sedinger et al. 1995). Brant therefore face a tradeoff between fidelity to nest sites and timing of nest initiation.

Dispersal of female brant from natal nest sites was directional, towards the northern portion of the colony. I observed no evidence that brant returned to natal sites in subsequent nesting attempts. Natal dispersal was therefore a mechanism for expansion of the colony.

Despite the high probability of site fidelity observed in this study and previous studies of waterfowl populations (Anderson et al. 1992), few studies have documented an advantage to fidelity or a disadvantage of dispersal (but see Dow and Fredga 1983, Gauthier 1990). Potential advantage of site fidelity mediated through site familiarity include higher nest success, improved feeding efficiency, and greater reproductive output (Lack 1954). My tests of advantages of site fidelity provided equivocal results. Although I noted no relationship between nest success or timing of nest initiation and dispersal distance, clutch size declined with dispersal distance. I was unable to separate the effects of bird quality from the proximate effects of dispersal. Environmental conditions and demographic status may be more important determinants of breeding performance than site fidelity. I suspect that brant may benefit from site fidelity during periods when they

can exploit knowledge of local food resources (i.e., brood rearing) (but see Cooch et al. 1993).

Philopatry and Genetic Structure of Populations: My estimates of breeding philopatry for brant exceeded all previously published estimates of return rates for waterfowl (see Anderson et al. 1992), but were similarly to estimates of philopatry that controlled for variation in survival and detection probabilities (Hepp et al. 1987, Szymczak and Rexstad 1991, Blums et al. 1996). Most previous studies of philopatry and dispersal patterns in waterfowl, however, were limited to single study site (Anderson et al. 1992) and based on inappropriate statistical models (Johnson et al. 1992). Probability of natal philopatry were lower than estimates of breeding philopatry. I observed among colony dispersal of both male and female brant.

Probability of both natal and breeding philopatry were female-biased. Lower probabilities of breeding philopatry of males than females probably resulted from males pairing with females from other colonies following loss of mate (Cooke et al. 1975, Lessels 1985). Rates of natal philopatry of male brant were similar to probabilities expected under a hypothesis of random mating relative to colony of origin. Therefore, timing of pair formation and a mate-defense mating systems were more likely mechanisms for sex-biased differences in philopatry (Greenwood 1980, Rohwer and Anderson 1988) than genetic mechanisms based on hypotheses of positive or negative assortative mating (Shields 1982, Shields 1983, Greenwood 1987, Pusey 1987).

Probability of natal philopatry for females increased with age because probability

of temporary emigration declined. For females, probability of natal philopatry was density-dependent. Increased probability of permanent emigration by females from Tutakoke reflects both emigration to other colonies and permanent nonbreeding.

Although largely male mediated, dispersal among colonies that I studied was extensive and nearly ubiquitous. The rates of dispersal observed in these populations has likely implications for the population genetic structure of brant. Effects of gene flow on population genetic structure are difficult to quantify (Rockwell and Barrowclough 1987). Homogenizing effects of gene flow are counterbalanced by diversify forces of genetic drift, mutation, and natural selection (Mayr 1942). Observations of dispersal among populations may not represent gene flow (i.e., effective dispersal) because emigrant genes may not be incorporated in recipient populations. In addition, effects of gene flow on population genetic structure are influenced by extent of genetic divergence among recipient and donor populations, effective population size of the destination colony, and the degree to which emigrants are a random sample of the gene pool of their natal colony (Endler 1977, Rockwell and Barrowclough 1987). Nevertheless, because of high probabilities of female philopatry I expect that the maternally inherited portion of the genome (i.e., mitochondrial DNA) will exhibit geographic concordance if brant populations were not recently diverged (Avise et al. 1992). Male-mediated gene flow may affect fitness components of brant populations (see Rockwell et al. 1987), however, these effects may be minor as life-history traits of brant are strongly influenced by environmental conditions (Sedinger and Flint 1991, Sedinger et al. 1995) suggesting low heritabilities of

these traits.

The extent of mixing among subpopulations of brant may warrant management of these birds as a single population. However, over-exploitation may have dramatic effects on viability of small (island) subpopulations (McCullough 1996), particularly Arctic colonies. Furthermore, density dependent rates of permanent emigration may not represent a source-sink relationship (Pulliam 1988), in which sink populations with low fitness are maintained by emigrants from source population with higher fecundity. Density-dependent rates of permanent emigration may reflect increased probability of nonbreeding rather than increased probability of dispersal. Subpopulations may therefore be subject to extinction or severe bottlenecks if these populations are over exploited.

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